

Neck Muscles in the Rhesus Monkey. II. Electromyographic Patterns of Activation Underlying Postures and Movements

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Corneil, Brian D., Etienne Olivier, Frances J. R. Richmond, Gerald E. Loeb, and Douglas P. Munoz. Neck muscles in the rhesus monkey. II. Electromyographic patterns of activation underlying postures and movements. *J Neurophysiol* 86: 1729–1749, 2001. Electromyographic (EMG) activity was recorded in ≤ 12 neck muscles in four alert monkeys whose heads were unrestrained to describe the spatial and temporal patterns of neck muscle activation accompanying a large range of head postures and movements. Some head postures and movements were elicited by training animals to generate gaze shifts to visual targets. Other spontaneous head movements were made during orienting, tracking, feeding, expressive, and head-shaking behaviors. These latter movements exhibited a wider range of kinematic patterns. Stable postures and small head movements of only a few degrees were associated with activation of a small number of muscles in a reproducible synergy. Additional muscles were recruited for more eccentric postures and larger movements. For head movements during trained gaze shifts, movement amplitude, velocity, and acceleration were correlated linearly and agonist muscles were recruited without antagonist muscles. Complex sequences of reciprocal bursts in agonist and antagonist muscles were observed during very brisk movements. Turning movements of similar amplitudes that began from different initial head positions were associated with systematic variations in the activities of different muscles and in the relative timings of these activities. Unique recruitment synergies were observed during feeding and head-shaking behaviors. Our results emphasize that the recruitment of a given muscle was generally ordered and consistent but that strategies for coordination among various neck muscles were often complex and appeared to depend on the specifics of musculoskeletal architecture, posture, and movement kinematics that differ substantially among species.

INTRODUCTION

Much work on simian head movement has focused on orienting behaviors (e.g., Crawford et al. 1999; Freedman and Sparks 1997) in an effort to extend work done on saccadic eye movements in head-restrained preparations. Studies of the saccadic system usually employ saccades themselves as an index of the underlying neural events and kinetics because the mechanics of this system are relatively intuitive. In contrast, head movements are generated by more than two dozen muscles

operating on a complex multiarticular linkage endowed with substantial inertia (Richmond and Vidal 1988; Winters 1988). The design and interpretation of experiments on such a system requires knowledge of its structural elements, which is provided in the companion paper on muscle morphometry (Richmond et al. 2001).

Chronically indwelling electrodes in animals provide the opportunity to assess reliably electromyographic (EMG) activity in muscles not accessible in humans. Studies in human neck muscles have generally relied on surface EMG from large, relatively superficial muscles (Dee and Zangemeister 1998; Hannaford et al. 1985; Keshner et al. 1989; Mayoux-Benhamou and Revel 1993; Mayoux-Benhamou et al. 1997; Zangemeister et al. 1982) or percutaneous EMG from only one or two muscles whose identities can be hard to determine (Mayoux-Benhamou et al. 1995). A broader range of muscles have been studied previously in cats (Keshner 1994; Keshner et al. 1992; Richmond et al. 1992; Thomson et al. 1994, 1996; Wilson et al. 1983), but the differing features of feline head-neck structure potentially limit the applicability of these results to primate studies. Previous studies in monkeys have recorded neck muscle EMG in a few neck muscles or during a restricted subset of head movements (Bizzi et al. 1971; Le Goff et al. 1992; Lestienne et al. 1995, 2000). However, little systematic study to date has focused on the relationships between simian head kinematics and neck muscle activation during a more extensive sampling of neck muscles and head movements.

In this study, the spatial and temporal patterns of EMG activity were examined in a large number of neck muscles in monkeys free to move their heads. Head postures and movements were generated either in a trained protocol requiring gaze shifts to visual targets or were generated spontaneously during orienting, tracking, feeding, expressive, and head-shaking behaviors. The inclusion of the latter head movements increased the range of kinematic patterns beyond those which accompanied trained gaze shifts.

Some results have been reported previously in abstract form (Corneil et al. 1996, 1999).

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METHODS

Surgical and training procedures

Four male monkeys (*Macaca mulatta*) weighing 5.4–9.1 kg were used in these experiments according to procedures approved by the Queen's University Animal Care Committee and the guidelines of the Canadian Council on Animal Care. Each monkey underwent two surgeries. In both, anesthesia was induced with ketamine hydrochloride and maintained with isoflurane. Antibiotics were administered pre- and postoperatively, and anti-inflammatories and analgesics were administered postoperatively.

In the first surgery, eye coils were implanted subconjunctivally (Judge et al. 1980) to monitor gaze (eye-in-space) position (Fuchs and Robinson 1966), and a head post was attached to the skull by way of a dental acrylic pedestal that also held the leads and connectors. Monkeys were trained on oculomotor tasks (see following text) prior to the second surgery. In the second surgery, chronically indwelling EMG electrodes were implanted in neck muscles using a similar approach to that described in cats (Richmond et al. 1992). Muscle layers were separated from the dorsal midline raphe to gain access to the cleavage planes between muscles. Up to 12 muscles in each monkey were implanted using bipolar epimysial patch electrodes or bipolar intramuscular hook electrodes (Table 1). Full details of the electrode design have been described previously (Loeb and Gans 1986). In both, the recording contacts were 3 mm long, separated by ~3 mm and were oriented perpendicularly to the long axis of the muscle fiber fascicles. Some muscles implanted with intramuscular hook electrodes were shielded from the potential cross-talk of adjacent muscles by suturing Silastic sheeting to the overlying fascia. Muscle layers were approximated with a midline closure. A ground wire consisting of a single, partially bared loop of Teflon-coated, multistranded stainless steel was stitched to subcutaneous fascia. The leads from all implanted electrodes were tunneled subcutaneously to the acrylic skull pedestal and soldered to multipin connectors. By the second or third postoperative day, all animals appeared to be making normal head movements.

TABLE 1. Recorded muscles and abbreviations

Muscle	Monkey l	Monkey f	Monkey z	Monkey r
Obliquus capitis inferior (OCI)	l r	L R	l r	l r
Splenius capitis (SP cap)	L R	L R	x r	l r
Complexus (COM)	L R	L	r	l r
Obliquus capitis superior (OCS)	L r			
Longissimus capitis (LONG cap)	l R			
Sternocleidomastoid (SCM)		l r	r	
Biventer cervicis (BC)		L	r	l x
Rhomboideus capitis (RH cap)		L R	l	
Rectus capitis posterior major (RCP maj)		X	l	l r
Trapezius (TRAP)*		L	l	
Atlanto-scapularis anterior (AS ant)			l	
Atlanto-scapularis posterior (AS post)			l	

The side of the implanted device is designated by either L or l for left muscles and R or r for right muscles. X or x indicates a muscle that was excluded from analysis because of electrode failure. Upper case letters denote muscles that were implanted with patch electrodes, lowercase letters denote muscles that were implanted with intramuscular hook electrodes. See the companion paper (Richmond et al. 2001) for morphometric descriptions of these muscles. * The rostral-most compartment of TRAP was implanted.

Experimental procedures

Prior to EMG recording, the monkey was placed in a primate restraining chair designed to permit unrestrained head movements. Monkeys l and f were placed in a commercially available primate chair (Crist Instruments), modified to allow attachment of a body harness which permitted approximately $\pm 45^\circ$ of trunk rotation in the horizontal plane. Monkeys z and r were placed in a custom-made primate chair that permitted the monkeys to be tethered to the chair via a customized primate vest (Lomir Biomedical). This arrangement was more effective at preventing trunk rotation (estimated to be $\pm 10^\circ$) without restraining the head or neck. We saw no evidence that patterns of EMG activities differed in the two chairs, but a wider range of the head positions was typically achieved when using the custom-made chair.

Spontaneous sessions were recorded in monkeys l, f, and z in which volitional head movements were generated during a variety of orienting, tracking, feeding, or expressive behaviors in a well-lit room. Experimenters in the room encouraged head movements by displaying food, verbalizing, or hand-waving; desired movements were rewarded with food and verbal praise. The animals appeared to behave normally and showed no signs of stress.

Monkeys z and r worked in *trained sessions* in a dark, sound-attenuated room, performing an oculomotor task in which they had been trained previously. Stimuli consisted of 60 light-emitting diodes (LEDs) arranged at the front and both sides of the monkey, spanning 90° to the right and left of center, and 45° above and below center. To receive a liquid reward, the monkey had to fixate the central LED for ≥ 500 ms, look to one of eight randomly selected peripheral LEDs illuminated as the central LED was extinguished, fixate the peripheral LED for ≥ 500 ms, look back to the central LED illuminated as the peripheral LED was extinguished, and fixate the central LED for ≥ 500 ms. The locations of the eight peripheral LEDs were varied between blocks, allowing a considerable range of head postures and centrifugal (away from midline) and centripetal (toward midline) movements to be obtained over several days.

Data collection and analysis

A flexible ribbon-cable that did not interfere with head movements linked the EMG connector(s) to the signal processing electronics. The signal-processing architecture used for monkey l was different from that used for the other monkeys. Briefly, all EMG signals for monkey l were amplified differentially, bandwidth filtered (100–5,000 Hz) and recorded on an FM tape recorder. Segments of interest were rectified and integrated into 3.3-ms bins and digitized at 3.3 ms (see Thomson et al. 1994 for details). Sessions for monkey l were videotaped at 60 fields/s using two shuttered cameras placed above and to one side of the monkey, allowing estimation of the position of the head on the body.

For monkeys f, z, and r, digitized signals of the EMG activity and the gaze (eye-in-space) and head (head-in-space) positions derived from the magnetic coil system were recorded simultaneously. The coil system (CNC Engineering) yokes the two horizontal fields together, hence the relationships between induced current and horizontal coil position was linear over a range of $\pm 90^\circ$ from center. The search coil and a tube for the fluid reward were secured to the head pedestal and did not interfere with normal head movements or vision. The EMG ribbon-cable led to preamplifiers and low-pass filters (MAX274 integrated IC filter, $f_c = 8$ kHz, roll-off = 24 dB/octave, Maxim Electronics) that filtered out the coil frequencies. Data were then fed into an Analog Preprocessor and Timer (Aztec Associates) that enabled computer-programmable amplification, filtering (100- to 5,000-Hz bandwidth), rectifying and digitizing of the signals into 2-ms bins. The amplification was adjusted for different channels to yield a maximal peak-to-peak output voltage of ~5 V. The amplitudes reported here correspond to raw EMG signals with ~10 times larger

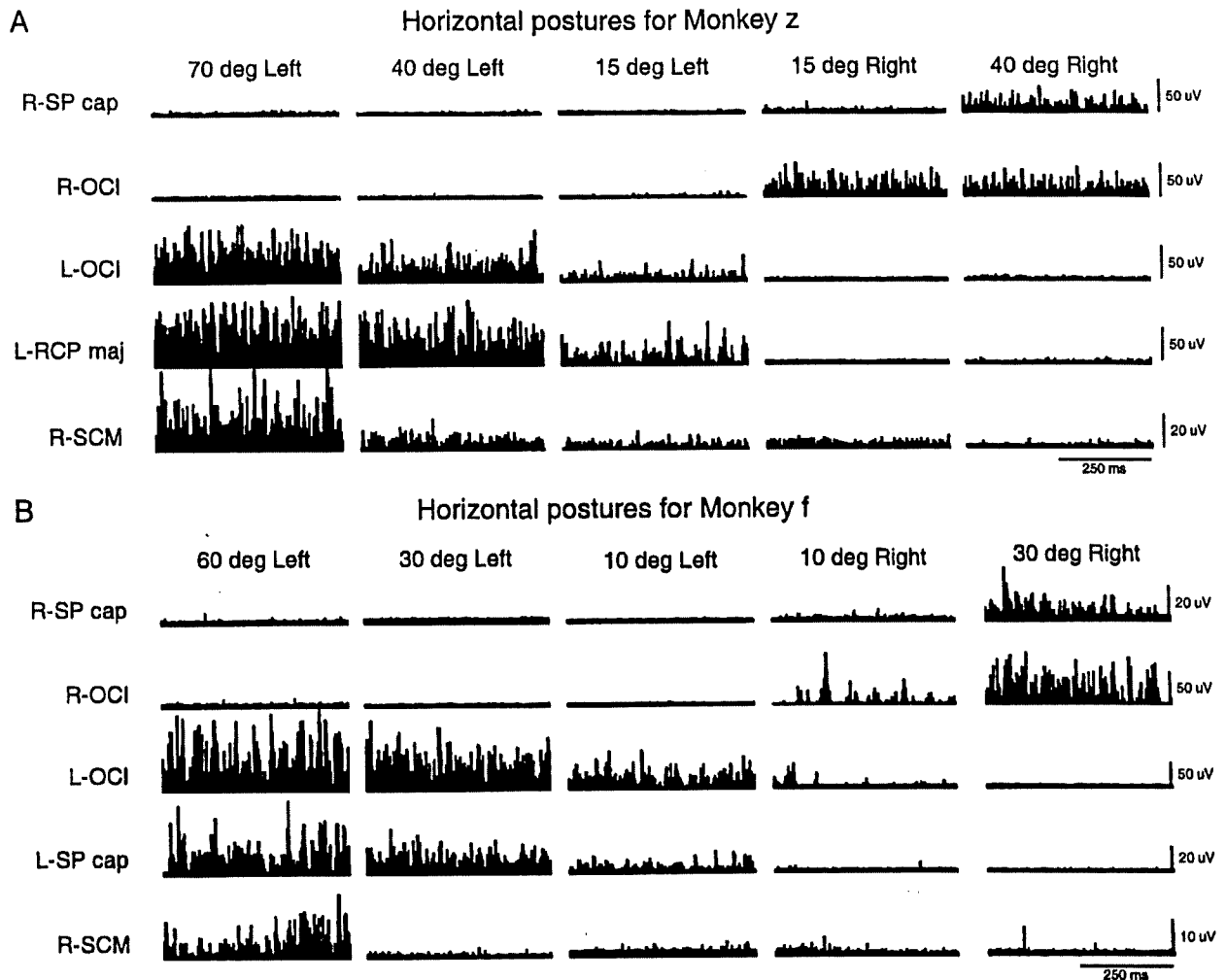


FIG. 1. Electromyographic (EMG) patterns in 4 muscles whose activity varied with different turned postures. Records are obtained from trained sessions in *monkey z* (A) and spontaneous sessions in *monkey f* (B) over a range of postures turned to the left or right. Each record is 500 ms long. SP cap, splenius capitis; OCI, obliquus capitis inferior; RCP maj, rectus capitis posterior major; SCM, sternocleidomastoid. The R or L in front of each muscle abbreviation denotes the right or left muscle, respectively.

peak-to-peak amplitudes (Bak and Loeb 1979). Bins with amplitudes $\leq 5 \mu\text{V}$ were assumed to represent noise; this value was generally used as a limit below which the muscle was classed as silent and data points were excluded from correlation analyses. The EMG signals and the horizontal and vertical gaze and head position signals were digitized at 500 Hz with a Pentium computer running a real-time data acquisition system (REX version 5.4) (Hays et al. 1982). The behavioral sessions for *monkeys f*, *z*, and *r* were videotaped using a single infra-red camera in conjunction with an infra-red light source, synchronized by a software-controlled trial counter placed in the camera's field of view.

Behaviors of interest from spontaneous sessions (*monkeys l*, *f*, and *z*) were selected by inspecting the videotaped sessions. In the trained sessions (*monkeys z* and *r*), analyses were performed only on correct trials. Segments or trials in which the monkey adopted a posture unsuitable for these experiments (i.e., head resting on neck plate or torso twisted away from the frontal plane) were not analyzed. Head velocity and acceleration traces were obtained by differentiation and double-differentiation, respectively, of position signals. The onsets and offsets of orienting head movements were determined when the head velocity crossed a $10^\circ/\text{s}$ threshold. The onset and offset of translating or torsional movements were determined by examining the videotaped sequences along with the head position signals. The "zero"

position to which both horizontal and vertical planes were referenced occurred when the monkey's head was pointed straight ahead without inclination or declination, such that the search coil mounted on the head, and hence the frontal plane of the head, was oriented parallel to the front plane of the coil frame.

When appropriate, the temporal aspects of the EMG signals in some muscles were determined by quantifying the time of activation and silencing. Although no strict quantitative criteria were used, sudden changes in EMG activity levels were easily delineated. To quantify the magnitude of the EMG response during stable postures, the EMG signal was averaged over the duration of the postural segment. To quantify EMG response magnitude during head movements, the EMG signal was first smoothed with a 50-ms running average (i.e., ± 25 ms from the point under consideration), selected because it approximates the dynamics of muscle-force development and reduces the variability arising from the stochastic nature of the EMG signal (Loeb and Gans 1986). EMG response magnitude was quantified by taking the peak of this smoothed signal over a period ranging from 75 ms before movement onset to the time of peak head velocity to capture an estimate of the EMG contributing to the accelerational torques required to produce the movement. For very transient EMG signals during rapid head movements in which this method was inappropriate (e.g., bursts in

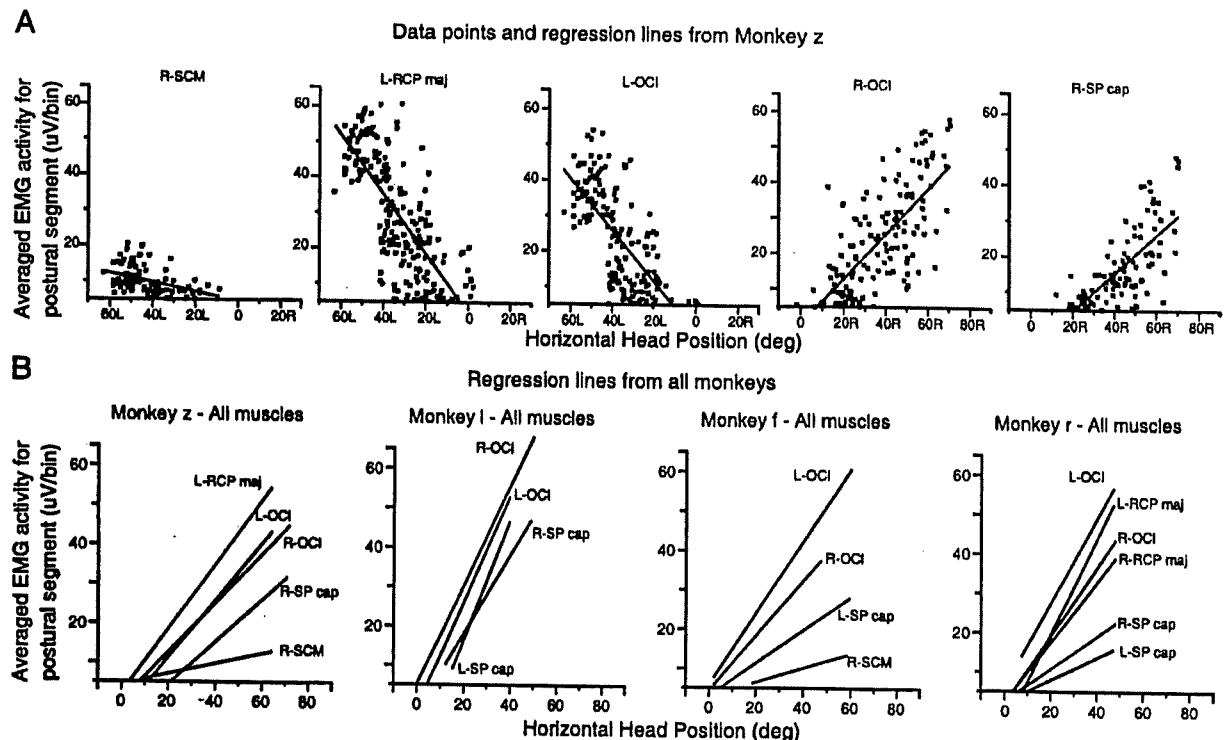


FIG. 2. Correlation of mean EMG activity with eccentricity of turned posture. A: data for 5 muscles from monkey z from trained sessions: R-SCM, L-RCP maj, L-OCI, R-OCI, and R-SP cap. Each point in A plots the level of EMG activity averaged over a single stable postural segment (duration range, 250–950 ms; mean, 410 ms) as a function of the eccentricity of the turned posture. Points with mean EMG values $<5 \mu\text{V}$ are not shown since such values were associated with negligible muscle recruitment. —, in A and B, statistically significant ($P < 0.05$) linear regression lines for the points shown. B: composite plot of the regression lines for muscle activities related to the eccentricity of turning for all monkeys using data obtained from trained sessions (monkeys z and r) or spontaneous sessions (monkeys l and f). The regression lines for muscles related to leftward turned postures have been flipped to allow for comparison with muscles related to rightward turned postures so that positive values on the abscissa represent the preferred direction of the muscle. Only turned postures in which the head posture in the vertical plane was within $\pm 10^\circ$ of vertical center were included.

Fig. 6), the magnitude of the EMG signal was obtained by integrating the area under the EMG curve, without smoothing.

Overall, we analyzed a total of 1,053 postural segments (110 from monkey l, 67 from monkey f, 670 from monkey z, 206 from monkey r), 2,311 movement segments (359 from monkey f, 1,811 from monkey z, 131 from monkey r), and 70 complex segments composed of multiple movement phases (i.e., head shakes, translations, feeding behaviors, etc.; 57 from monkey f, 13 from monkey z). Movement data from monkey l were not analyzed quantitatively, but movements were inspected to ensure that the EMG patterns were qualitatively similar to results from the other monkeys. For the sake of simplicity given the number of recorded muscles, analyzed data from a given muscle are presented only if that muscle served as an agonist or antagonist to the posture or movement in question.

RESULTS

All monkeys held a variety of postures and generated head movements during either spontaneous (monkeys l, f, and z) or trained (monkeys z and r) sessions. It was impossible to obtain perfectly comparable records from monkey to monkey because different muscles were implanted (Table 1), but consistent patterns of neck muscle activation were observed across multiple segments and monkeys. To illustrate this point, most figures display multiple postures or movements from monkey z and one of either monkey f or r. Small differences were often seen in the activities of muscles from one sequence to the next;

where appropriate, we identify idiosyncratic observations to distinguish them from the more general patterns. We present EMG patterns associated with postures and movements in the horizontal plane, postures and movements in the vertical plane, and during forward translations or vigorous head shakes.

EMG activity during postures or movements in the horizontal plane

TURNED POSTURES. All monkeys frequently held their heads in turned postures. The eccentricity of head postures analyzed here ranged up to $\pm 70^\circ$ from center for monkey z, $\pm 60^\circ$ for monkey f, $\pm 50^\circ$ for monkey r, and $\pm 40^\circ$ for monkey l. EMG activity was negligible in all recorded muscles when the head was held at the central “zero” position and when the head was turned away from the preferred direction of the muscle. Modestly turned postures $<20^\circ$ from center were associated with consistent activity only in the ipsilateral suboccipital muscles obliquus capitis inferior (OCI) and rectus capitis posterior major (RCP maj) (Fig. 1, A and B, 3rd and 4th columns). Larger turned postures ~ 20 – 50° from center were associated with stronger activation in the ipsilateral suboccipital muscles, and a lower level of activity in ipsilateral splenius capitis (SP cap; Fig. 1, A and B, 2nd and 5th columns). These same ipsilateral muscles were activated strongly in extreme postures $>50^\circ$ from center, and sternocleidomastoid (SCM) contralateral to the side of turning also became active (Fig. 1, A and

B, 1st column). The EMG activity during turned postures was usually $<50 \mu\text{V}/\text{bin}$ for the suboccipital muscles and $<20 \mu\text{V}/\text{bin}$ for the larger muscles, although these values were exceeded at extreme postures.

We computed the mean level of EMG activity during stable postures from either trained sessions (*monkeys z and r*) or spontaneous sessions (*monkeys l and f*). Figure 2A illustrates the results of this analysis for *monkey z*. Some variability in the EMG levels in Fig. 2A may be related to small trunk or shoulder rotations or torsional head rolls, which could alter the head-re-body position without altering the position of the head coil in space. The suboccipital muscles (Fig. 2A, middle 3 columns) were recruited consistently when the head was held only a few degrees away from center. Activation in ipsilateral SP cap (Fig. 2A, rightmost column) and contralateral SCM (Fig. 2A, leftmost column) was observed in progressively more eccentric head positions. Similar patterns of neck muscle activation were observed in the other monkeys (Fig. 2B).

TURNING MOVEMENTS. Muscle recruitment during trained sessions. The same muscles active during turned postures (OCI, RCP maj, SP cap, and SCM) were recruited synchronously ~ 10 – 50 ms before head movements during trained gaze shifts (Fig. 3). Suboccipital muscles OCI and RCP maj were active during small turns (Fig. 3, A and C), and the larger muscles SP cap and SCM were additionally active during larger turns (Fig. 3, B and D). Occasionally, this initial activation was a phasic burst followed by lower tonic levels typical of the posture held at the end of the movement (e.g., Fig. 3, A and C); in other segments, no distinct phasic burst was apparent (Fig. 3, B and D). Antagonist muscles whose mechanical turning actions were away from the turn were essentially not recruited (Fig. 3).

Centrifugal head movements generated during trained sessions were characterized by close linear correlations between movement amplitude, peak velocity and peak acceleration (Fig. 4, A and B for *monkey z*, C and D for *monkey r*). The relationship between amplitude and velocity, the head “main sequence” (Fig. 4, A and C), is commonly observed during head movements generated during orienting gaze shifts (Freedman and Sparks 1997; Zangemeister et al. 1981). These kinematic relationships were reflected in the close linear relationship of the EMG activities of agonist muscles to the peak velocity (and hence also to the amplitude and acceleration) of the head turn (Fig. 5). The sequence of muscle recruitment was qualitatively similar to that observed for progressively larger turned postures: suboccipital muscles were preferentially active during small slow turns, whereas larger, multiarticular muscles became active additionally during larger faster turns (*monkey z*: Fig. 5, A–F, *monkey r*: G).

Muscle recruitment during spontaneous sessions. Untrained head movements generated during spontaneous sessions (*monkeys l, f, and z*) exhibited a broader range of kinematics, with more dissociation between amplitude, velocity and acceleration, permitting us to identify spatiotemporal features of EMG recruitment associated with movements of varying kinematics. The 16 movements displayed in Fig. 6 were all obtained from spontaneous sessions and contrast the activation of agonist and antagonist OCI muscles. This figure is organized to facilitate the comparison of movements with similar amplitudes but different dynamics for two different monkeys. The EMG activation for the regularly paced movements in Fig. 6A was

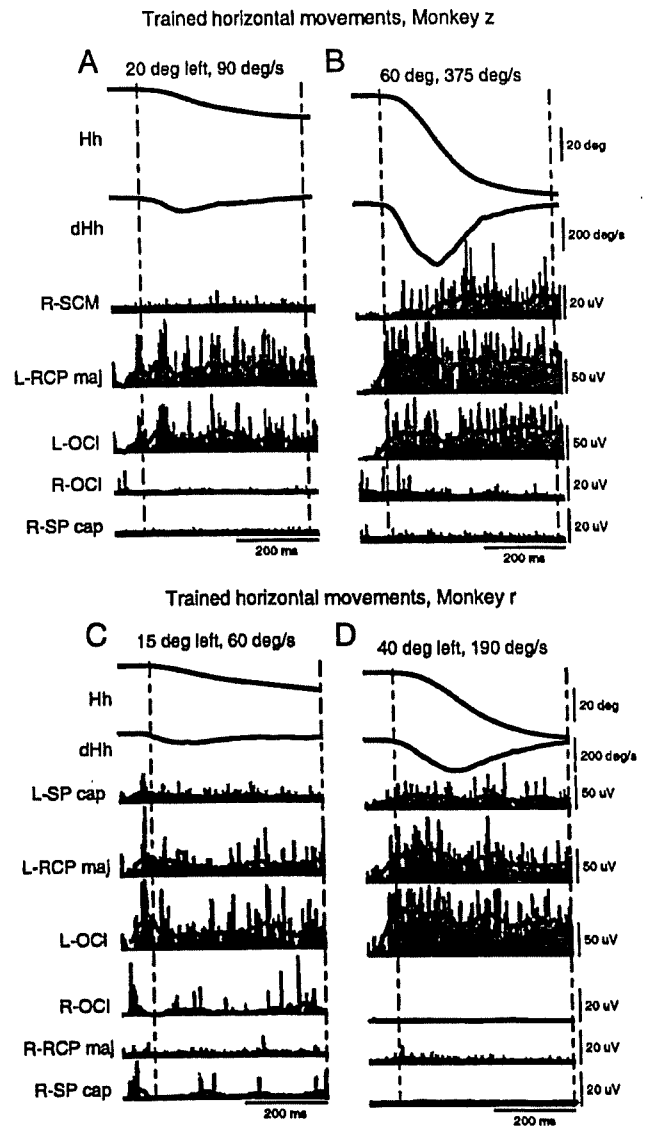
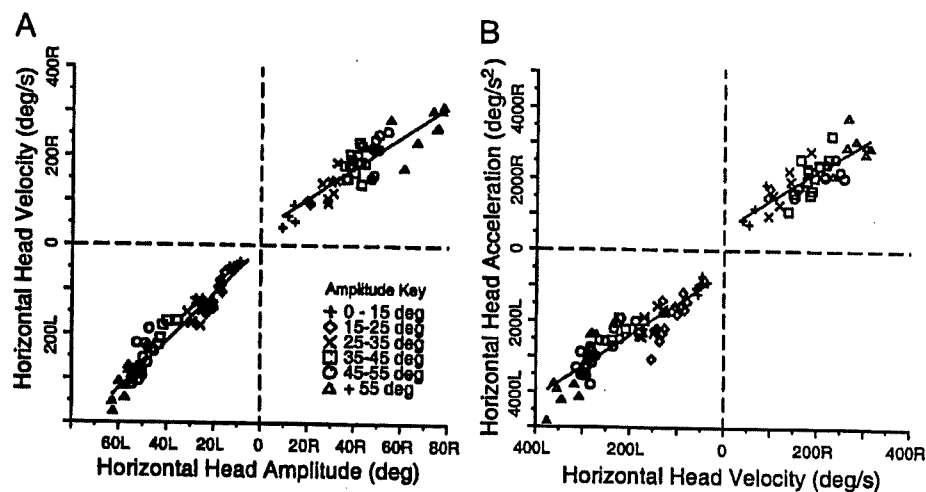


FIG. 3. Horizontal head position (Hh) and velocity (dHh) traces, and EMG patterns from *monkey z* (A and B) and *monkey r* (C and D) during 4 leftward turning movements. All data are obtained from head movements generated during trained sessions. Thick solid lines on the EMG traces denote the smoothed EMG activity averaged over ± 25 ms (see METHODS); peak levels of EMG activity for later analyses are derived from this smoothed activity. Vertical dashed lines in each figure delineate the onset and offset of each turn.

qualitatively similar to that which accompanied head movements during trained gaze shifts: agonist activity was present in the absence of antagonist activity. In contrast, during the very abrupt movements in Fig. 6B that depart markedly from the kinematic relationships shown in Fig. 4, EMG activities had reciprocally phasic profiles in which the initial phasic burst of the ipsilateral agonist muscle was followed some 30–50 ms later by a phasic burst in the contralateral antagonist muscle. Commonly, the reciprocal agonist and antagonist bursts adopted a triphasic or multiphasic profile of multiple bursts as the head settled into the turned posture (e.g., 2nd to 4th columns in Fig. 6B, 1st and 3rd columns of Fig. 6D). These subsequent bursts were not easily related to movement kinematics.

The magnitude of the initial agonist and antagonist bursts

Trained horizontal movements, Monkey z



Trained horizontal movements, Monkey r

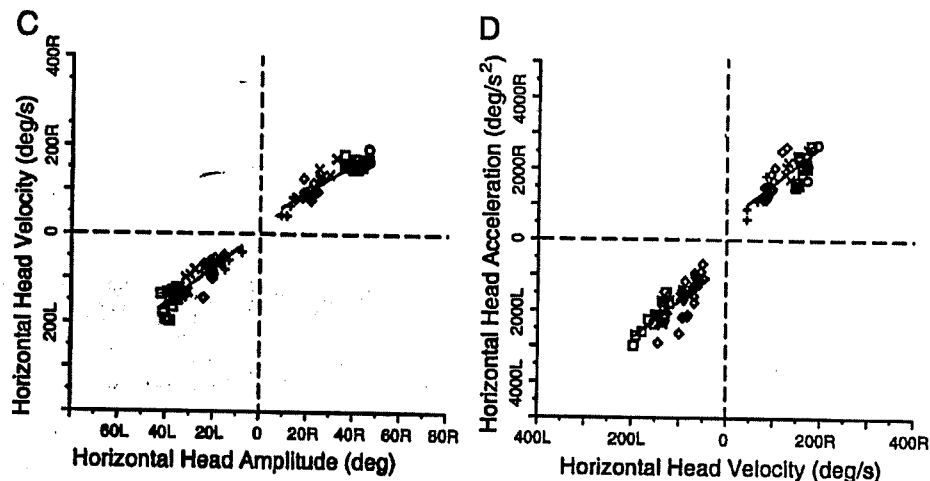


FIG. 4. Relationship of the kinematics of head turns associated with trained centrifugal, horizontal gaze shifts in *monkeys z* (A and B) and *r* (C and D). A and C correlate peak velocity to movement amplitude; B and D correlate peak acceleration to peak velocity. The different symbols denote various head movement amplitudes, as indicated in the key. Solid lines denote statistically significant linear regression lines ($P < 0.05$). Only trials in which the initial head position was within 10° of center and in which the movement deviated $<20^\circ$ of angular deviation from horizontal contributed data to this figure.

related well to the dynamics of the head movement. Figure 7 quantifies the area under the EMG burst in the agonist and antagonist OCI muscles as a function of the peak acceleration of the head during spontaneous sessions compared with the accelerations observed during regularly-paced movements (Fig. 7, gray regions). For each vertical line in Fig. 7, the lengths above and below the dashed zero line denote the magnitudes of the agonist and antagonist bursts, respectively, for a given movement. Large bursts in the antagonist muscle only accompanied head movements that accelerated faster than regularly paced head movements and increased progressively in magnitude for movements accelerating at more than $\sim 3,000^\circ/\text{s}^2$. Not surprisingly, agonist muscle activity accompanied all head movements and increased in magnitude for faster movements. Similar relationships between agonist and antagonist burst magnitudes and head acceleration were observed in RCP maj, SP cap, and SCM.

Centrifugal versus centripetal turning movements. The spatiotemporal patterning of neck muscle activation varied not only with the size and dynamics of the turn, but also with the initial position of the head. Figure 8 compares representative centrifugal (*monkey z*: Fig. 8, A and B; *monkey f*: E and

F) and centripetal (*monkey z*: Fig. 8, C and D; *monkey f*: G and H) head turns, matched approximately for size and speed but starting from different initial head positions. Synchronous activation in ipsilateral agonist muscles preceded the onset of centrifugal turns (Fig. 8, A, B, E, and F). In contrast, a distinct spatial and temporal EMG activation sequence was observed during centripetal turns. First, centripetal movements were preceded by silencing of the tonically active contralateral muscles that contributed to the initial eccentric position (Fig. 8, C, D, G, and H). Second, activation in ipsilateral atlantocapularis anterior (AS ant) preceded or was synchronous with the start of centripetal turns (Fig. 8C; this muscle was only implanted in *monkey z*). Notably, AS ant was rarely active during centrifugal turns (Fig. 8A) and was not active during turned postures. Third, activation in ipsilateral OCI occurred only just before or slightly after the onset of centripetal turns but was delayed relative to the time of onset for centrifugal turns (Fig. 8, C, D, G, and H). Fourth, a burst in ipsilateral SP cap lagged the burst in ipsilateral OCI by up to 50 ms or more (Fig. 8, D, G, and H).

We studied systematically the temporal sequences of

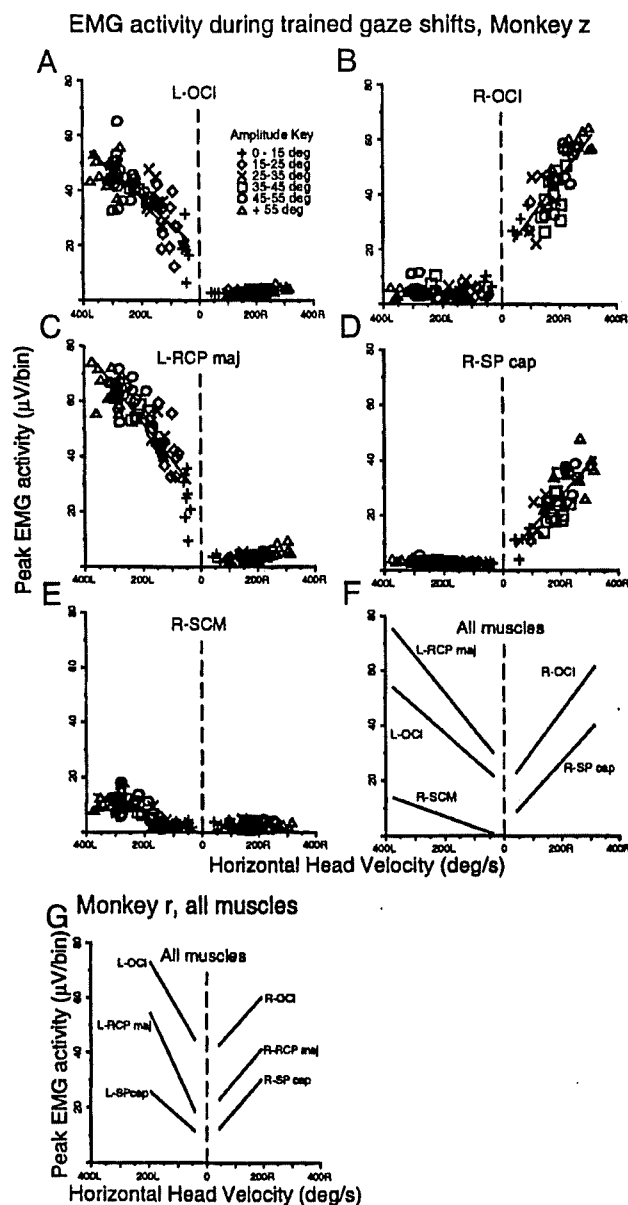


FIG. 5. Relationship of EMG activity to peak head velocity during trained centrifugal, horizontal gaze shifts in monkeys *z* (A–F) and *r* (G). Data obtained from the same set of movements as in Fig. 4, using the same symbol key to denote head movement amplitude. Solid lines denote statistically significant ($P < 0.05$) linear regression lines. A–E plot the peak smoothed EMG values for each trial vs. peak horizontal head velocity. The EMG activity was smoothed as shown in Fig. 3, and the peak EMG activity was taken from the period extending 75 ms before movement onset to the time of peak head velocity (see METHODS). The regression lines for each muscle are summarized in F for monkey *z*, and in G for monkey *r*.

EMG activity depending on initial head position in monkey *z*, which generated enough similarly sized turns from different initial head positions to permit analysis (monkey *f* did not contribute enough data to permit a similar analysis). Figure 9 plots the relationships between the time of activation or silencing of EMG activity and the onset of the turn as a function of initial horizontal head position. Activation in ipsilateral OCI was delayed progressively relative to the onset of the turn when turns began at more eccentric initial positions (Fig. 9, A and B). This resulted in an increasing lag

between the activation of ipsilateral OCI relative to the silencing of contralateral OCI (Fig. 9, C and D). The more eccentric the initial head position, the greater the lead of the burst in ipsilateral AS ant (Fig. 9E) and the greater the lag of ipsilateral SP cap activation (Fig. 9F) relative to the burst in ipsilateral OCI. Although the relationships shown in Fig. 9 were somewhat variable (perhaps due to small body or shoulder rotations or torsional head rolls), all were significant at the $P < 0.05$ level.

EMG activity during postures or movements in the vertical plane

VERTICAL HEAD POSTURES. All monkeys held their heads in different vertical postures, but the range of postures varied. Monkeys *f*, *l*, and *r* held vertical head postures ranging from 30° in inclination to 20° in declination. Monkey *z* held a wider range of postures from 55° in inclination to 50° in declination. The analysis of head postures in the vertical plane was more difficult than in the horizontal plane because some muscles active in vertical postures were also active in turned postures (e.g., RCP maj, SP cap, and SCM). Further, our implantation regime was not identical in all monkeys, hence we occasionally report results obtained from only one monkey.

In all four monkeys, very little activity was recorded when the head was in the central position (Fig. 10, 3rd column; the R-OCI activity in Fig. 10A is due to a small rightward turn). Complexus (COM) became increasingly active as head inclination increased, whereas biventer cervicis (BC), which lies immediately medial to COM, did not display strong tonic postural activity related to head inclination (Fig. 10A, 1st and 2nd column). Obliquus capitis superior (OCS, monkey *l* only) and RCP maj (Fig. 10A, monkeys *z* and *r*) were also recruited when the head was inclined modestly. Rhomboideus capitis (RH cap) was recruited with increasing head inclination in monkey *f* (Fig. 10B, 1st and 2nd column) but not monkey *z* (data not shown). SP cap (3 monkeys) and AS ant (monkey *z* only) also became increasingly active at progressively larger angles of inclination (Fig. 10, A and B). OCI was recruited only at extreme angles of inclination (Fig. 10A, 1st column). Maximal activation of all muscles when the head was held in an inclined posture seldom exceeded 50 μ V/bin.

The pattern of muscle activation for declined head postures varied between animals but generally included low activity levels in at least one head extensor muscle. In monkey *z* but not *f*, SCM was recruited for declined head postures (Fig. 10A, 4th column; the L-OCI and L-RCP maj activity was due to a small leftward turn). COM, but not BC, was active more consistently for declined postures in monkey *z* but not *f* (Fig. 10, 4th column). The only muscle in monkey *f* that showed any activity related to the degree of head declination was the rostral compartment of left trapezius (TRAP, Fig. 10B, 4th column), but this pattern was not observed for TRAP in monkey *z* (not shown). Thus recruitment patterns for declined postures were consistent within but not across monkeys, perhaps due to the differences in the magnitude of the declined postures.

An attempt was made to construct a plot similar to Fig. 2 for postures in the vertical plane using data from trained

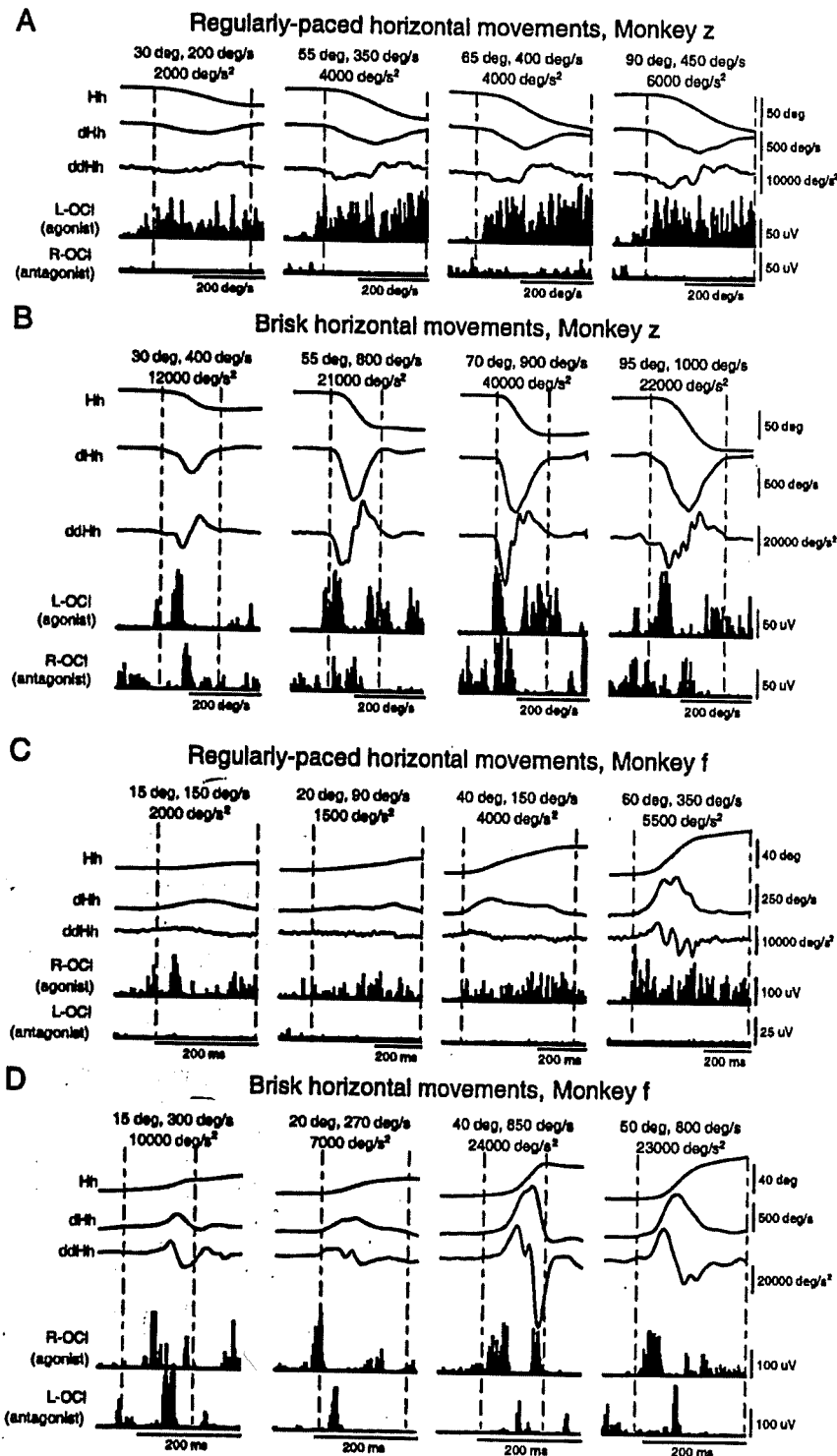


FIG. 6. Horizontal head position (Hh), velocity (dHh) and acceleration (ddHh) traces, and EMG patterns for 8 movements from each of *monkey z* (A and B) and *f* (C and D) during regularly paced (A and C) or brisk horizontal (B and D) movements. Same format as Fig. 3. All 16 head movements are derived from spontaneous sessions. The terms "regularly-paced" or "brisk" refer to head movements that are either kinematically similar or very different, respectively, to the trained head movements shown in Fig. 4. The figure is organized to enable comparison of approximately amplitude-matched movements. Thus the movements in A are comparable to the movements in the same column in B for *monkey z*, as are the movements in the respective columns of C and D for *monkey f*. Note the differences in the phasic nature of the profiles in B and D compared with the respective movements in A and C. Note as well that the time scale can differ for each movement, as do the scale bars for the kinematic and EMG signals.

sessions in *monkeys z* and *r*. However, the range of head postures spanned only $\pm 20^\circ$ in the vertical plane because monkeys tended to use eye movements more than head movements to fixate targets spanning $\pm 45^\circ$ in the vertical plane (see Freedman and Sparks 1997). This range was insufficient to provide a definitive plot of muscle activation versus head position in the vertical plane, particularly given the confounding dependency of EMG activity with turned postures in some muscles.

HEAD MOVEMENTS IN THE VERTICAL PLANE. Muscle recruitment during trained sessions. Figure 11 shows four inclining head movements and three declining head movements generated by *monkeys z* and *r*. For larger inclining movements (Fig. 11, A and E), moderate synchronous activation in COM and BC preceded the onset of the inclining movement by ~ 20 – 40 ms. Peak activation of these muscles during inclining movements never exceeded $50 \mu\text{V}/\text{bin}$. The activity profile consisted of an initial phasic component in both muscles, followed by a

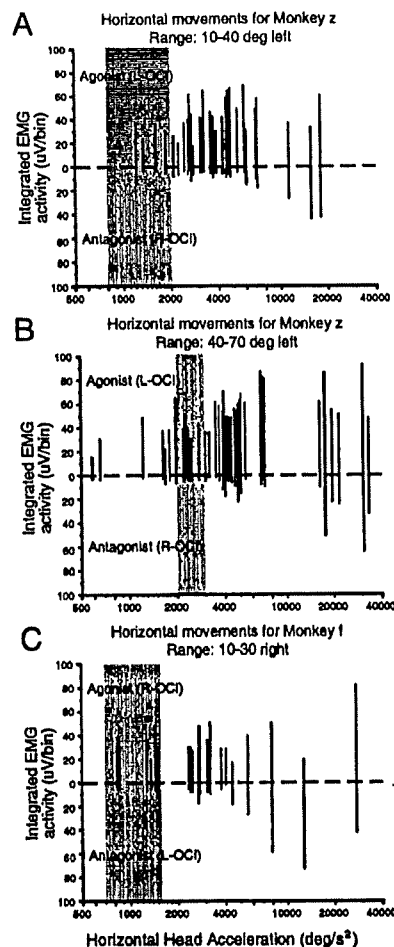


FIG. 7. Relationship between the integrated magnitude of the agonist and antagonist muscle activity to the peak acceleration of the head. All data are obtained from spontaneous sessions and are divided into movements between 10 and 40° left from *monkey z* (A), 40–70° left from *monkey z* (B), and 10–30° right from *monkey f* (C). Each solid vertical line represents data from a single head movement, plotted as a function of the peak head acceleration. The length above the dashed horizontal line expresses the integrated magnitude of the agonist burst, and the length below the dashed horizontal line expresses the integrated magnitude of the antagonist burst. The magnitude of the agonist muscle activity was calculated by integrating the area under the EMG signal from 50 ms before to 50 ms after the time of the peak agonist burst. The magnitude of the antagonist muscle activity was calculated by integrating the area under the EMG signal over 100 ms after the time of the peak agonist burst (see METHODS). The gray shaded boxes denote the range of accelerations typical for head movements during trained gaze shifts (the box in C was derived from data from *monkey r*). Note that significant antagonist activity is seen only for movements with accelerations much larger than the gray region, implying that antagonist activity accompanied only particularly brisk movements.

tonic component predominantly in COM typical of the posture held at the end of the movement. COM activity was bilateral in *monkey r*, but a similar determination could not be made for BC because the R-BC electrodes in this monkey failed. The magnitudes of the phasic components of COM and BC scaled to the size of the movement (Fig. 11, B and F). Further, EMG activity during inclining movements was limited to agonist muscles; antagonist muscles (R-SCM in Fig. 11, A and B) were not recruited.

The only muscle recorded in *monkey z* that was recruited during declining movements was SCM (Fig. 11D; not recorded

in *monkey r*). Activity in this muscle rarely exceeded 10 $\mu\text{V}/\text{bin}$ and appeared only during declining movements larger than 10–15° (Fig. 11C). No activity was observed in the antagonist muscles (COM and BC) during declining movements (Fig. 11, C, D, and G).

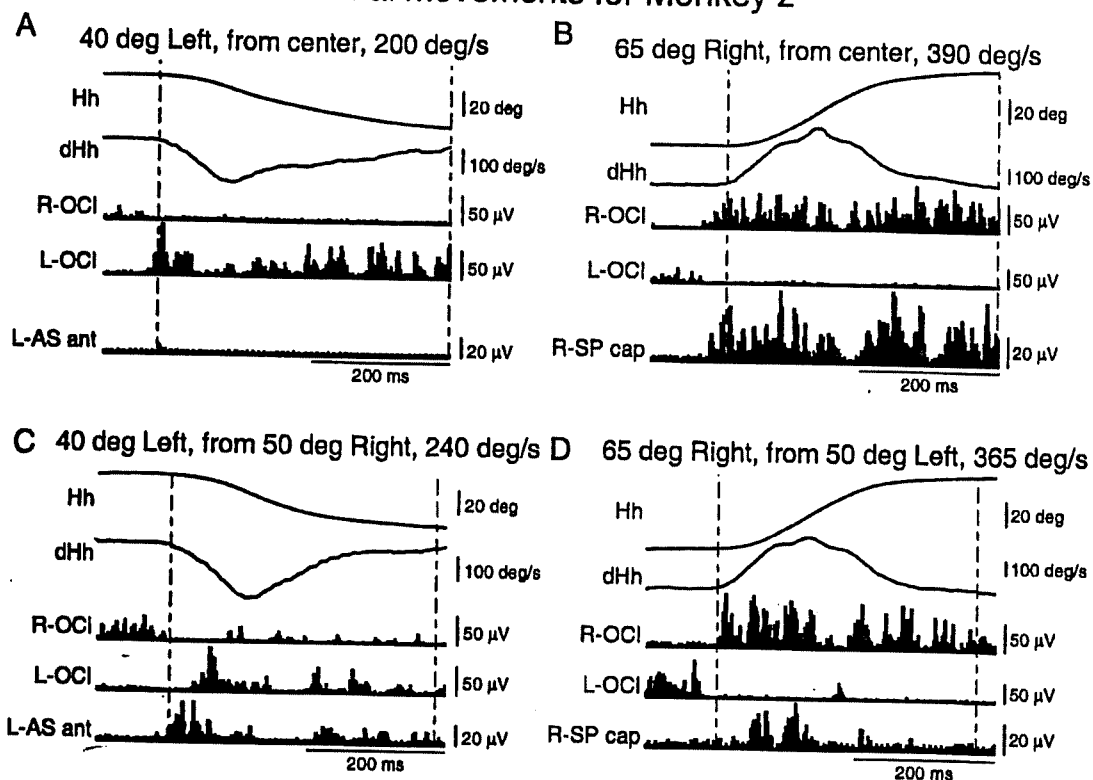
Like horizontal movements, the kinematics of vertical head movements during trained sessions displayed a “main sequence” relationship between peak head velocity and amplitude and a linear relationship between peak acceleration and peak velocity (Fig. 12, A, B, and G). Muscles tended to be recruited in proportion to these kinematics and only for directions in which they could contribute positive work: COM and BC were active during inclining head movements, and SCM was active during declining head movements (Fig. 12, C–F and H).

Muscle recruitment during spontaneous sessions. The spatial and temporal recruitment patterns of EMG activity during both inclining and declining movements in spontaneous sessions were affected by the more variable movement kinematics. There were not enough similarly sized movements of different dynamics to permit a quantitative analysis similar to that shown in Fig. 7, hence we present the EMG patterns from representative examples of head movements in the vertical plane and discuss the features that were common to movements of varying kinematics (Fig. 13). As with trained movements, slower inclining movements were preceded by moderate bursts of activity in COM and BC (Fig. 13, A, B, and D). Activity in muscles other than COM was observed in some but not all regularly paced inclining movements, probably due to small coincident turns. Particularly abrupt inclining movements were characterized by large phasic bursts that preceded movement onset by ~20–50 ms in BC and COM, and were also observed consistently in other muscles not recruited during the slower inclining movements, such as OCI, SP cap and RH cap (Fig. 13, C and E). RCP maj was typically activated more strongly or more extensively than OCI during inclining movements (Fig. 13C); this dissociation between RCP maj and OCI was unique to inclining as opposed to turning movements. Further, bilateral recruitment was commonly observed in SP cap and OCI even though this was never observed during turning movements. In *monkey f* in particular (Fig. 13E), an interval of silence followed these initial bursts, during which a burst of activity was commonly but not always observed in SCM and TRAP (Fig. 13E; the burst in R-OCI was most likely secondary to a small leftward turn).

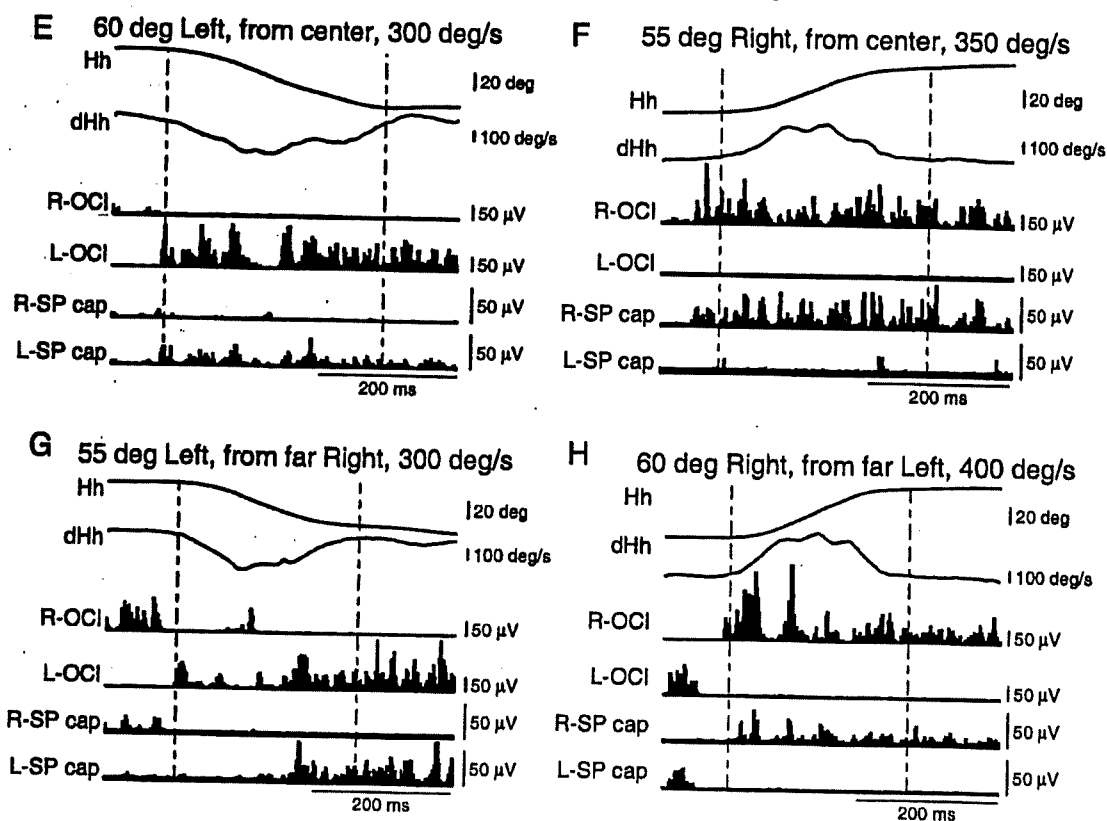
For declining head movements, large ($>20 \mu\text{V}/\text{bin}$) bursts of muscle activity were observed only during abrupt reversals of inclining movements (Fig. 14). Synchronous bursts of activity in extensors alternating with synchronous bursts of activity in flexors (particularly SCM and TRAP; shown for *monkey f*) preceded and presumably accounted for the triphasic peaks of acceleration (vertical lines in Fig. 14A). In contrast, little activity was present during the initial slow declining phase of the sequence illustrated in Fig. 14B even though its peak velocity was similar to that occurring during the subsequent reversal of a fast inclination. Further, these large bursts of activity were generated while the head was still inclining, presumably resulting in high force output in the actively lengthening fibers (see Zajac and Gordon 1989 for review).

Oblique inclining head movements. Inclining head movements with a turning component were typically associated with

Horizontal movements for Monkey z



Horizontal movements for Monkey f



Horizontal movements for Monkey z

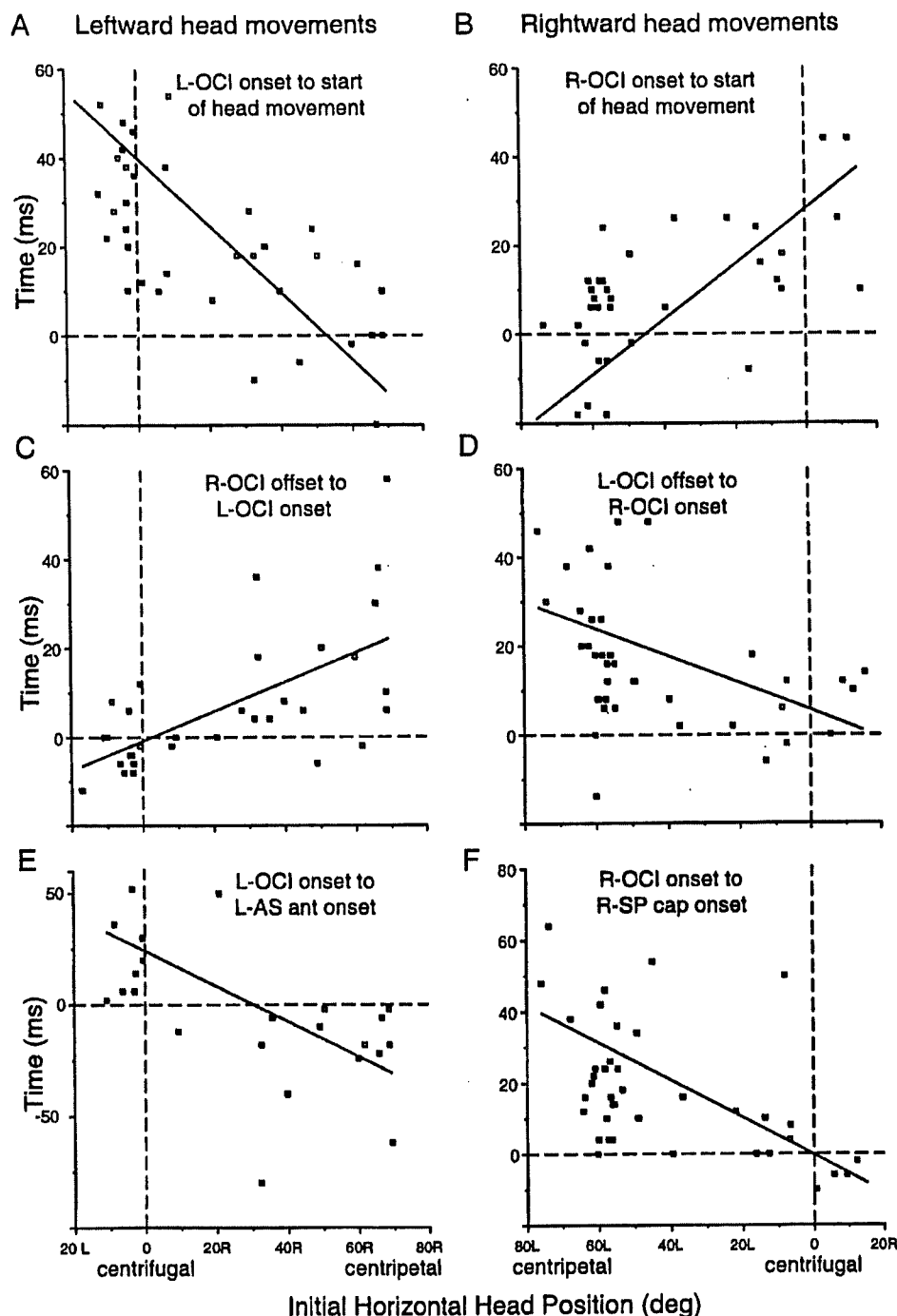


FIG. 9. Plots of the relationships between the relative timing of the onset of either the turn or the muscle as a function of initial horizontal head position, shown for either leftward head turns (A, C, and E) or rightward head turns (B, D, and F). All data are taken from 41 rightward and 36 leftward turns between 45 and 65° generated by *monkey z* during spontaneous sessions. Each point plots the value of the measure described in the graph title as a function of the initial horizontal head position, with positive values denoting initial head position to the right. Solid lines denote statistically significant ($P < 0.05$) linear regression lines for the points shown. Short, dashed lines denote the 0 values of the various axes. Slow head turns generated during tracking movements, extremely fast head turns, and head turns with vertical components $>10^\circ$ were excluded from this analysis. Each plot has a different number of points because each interval could not be measured for every turn.

activity in those ipsilateral muscles previously described to be strongly active during turns. In addition, COM, BC, and TRAP were more active during oblique inclining movements with contralateral as opposed to ipsilateral turning components (Fig. 15, A and B; oblique movements generated by *monkey r* were

not sufficiently eccentric to permit analysis). Activities in R-COM, R-BC, and L-TRAP were consistently larger for contralaterally directed oblique head movements (i.e., leftward for R-COM and R-BC, rightward for L-TRAP). Oblique declining movements were not analyzed similarly because the

FIG. 8. EMG patterns from *monkeys z* (A–D) and *f* (E–H) during large leftward (A, C, E, and G) or rightward (B, D, F, and H) turns in which the initial head position was either central (i.e., A, B, E, and F are centrifugal turns) or contralateral to the direction of the head turn (i.e., C, D, F, and H are centripetal turns). All data are taken from spontaneous sessions. The paired turns in A and C, B and D, E and G, and F and H were matched as closely as possible for kinematics. Same format as Fig. 3, except that the smoothed EMG average has not been applied.

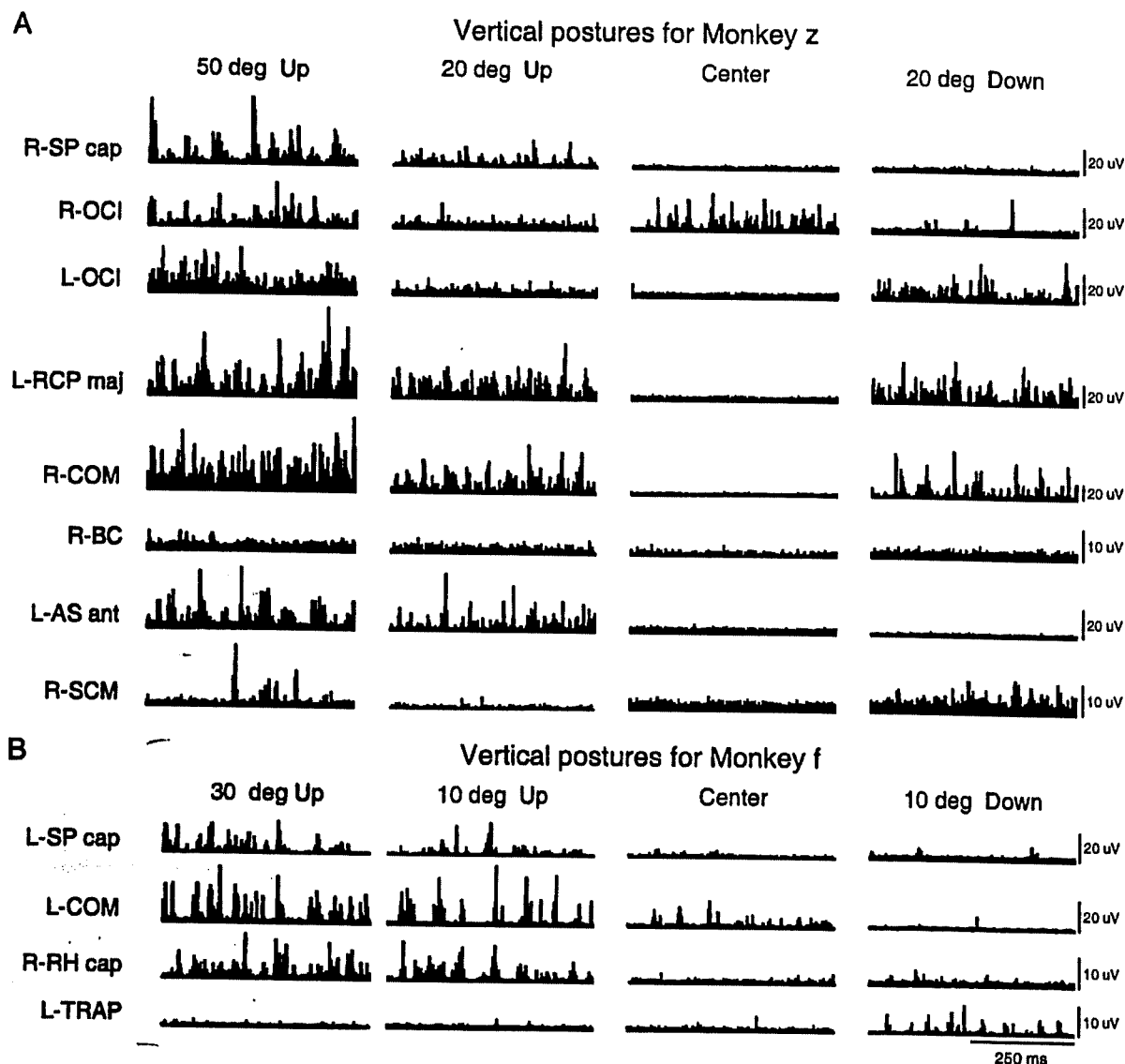


FIG. 10. EMG patterns from monkeys z (A) and f (B) in muscles whose activity varied for differing postures in the vertical plane. All data are from spontaneous sessions. Records are shown over a range of inclined and declined postures. Activity in some muscles (e.g., R-OCI in 3rd column of A, and L-OCI and L-RCP maj in 4th column of A) is due to small horizontal turns.

sample size was small, and the movements were more variable in their kinematics.

Feeding behaviors and head shakes

All monkeys moved their heads during eating or head shaking. The neck muscle activities during these movements attested to the larger range of highly orchestrated recruitment patterns that the monkey is capable of generating. During these movements, EMG patterns became quite specialized, and previously inactive muscles were recruited. We did not focus quantitatively on such movements because the magnetic search coil system provided calibrated measurements only for horizontal and vertical rotations, not for torsional rotations nor translational movements.

The EMG patterns shown in Fig. 16 were generated during a representative forward translation along the occipito-nasal axis,

which monkey f used to crane for offered food. The unique feature of this type of movement was the strong and increasing bilateral activation in SCM (Fig. 16), which occurred without significant activity in other muscles that were typically synergistic (OCI and SP cap) or antagonistic (COM) with SCM. TRAP was also active during this movement, although compared with SCM, the activity in TRAP was more discrete and did not increase greatly during the movement. Similarly strong activity was observed in R-SCM in monkey z during craning movements, although this muscle was not implanted bilaterally.

All monkeys spontaneously generated head-shaking sequences consisting of multiple oscillations in which the head was rapidly turned from one side to another over a period of 0.5–2 s. Head shakes were associated with the highest levels of EMG activity recorded in all muscles, regardless of whether the muscle linked the skull to the spinal column (OCI, SP cap, RCP maj, COM), the skull to the shoulder girdle (TRAP, RH cap), or the shoulder

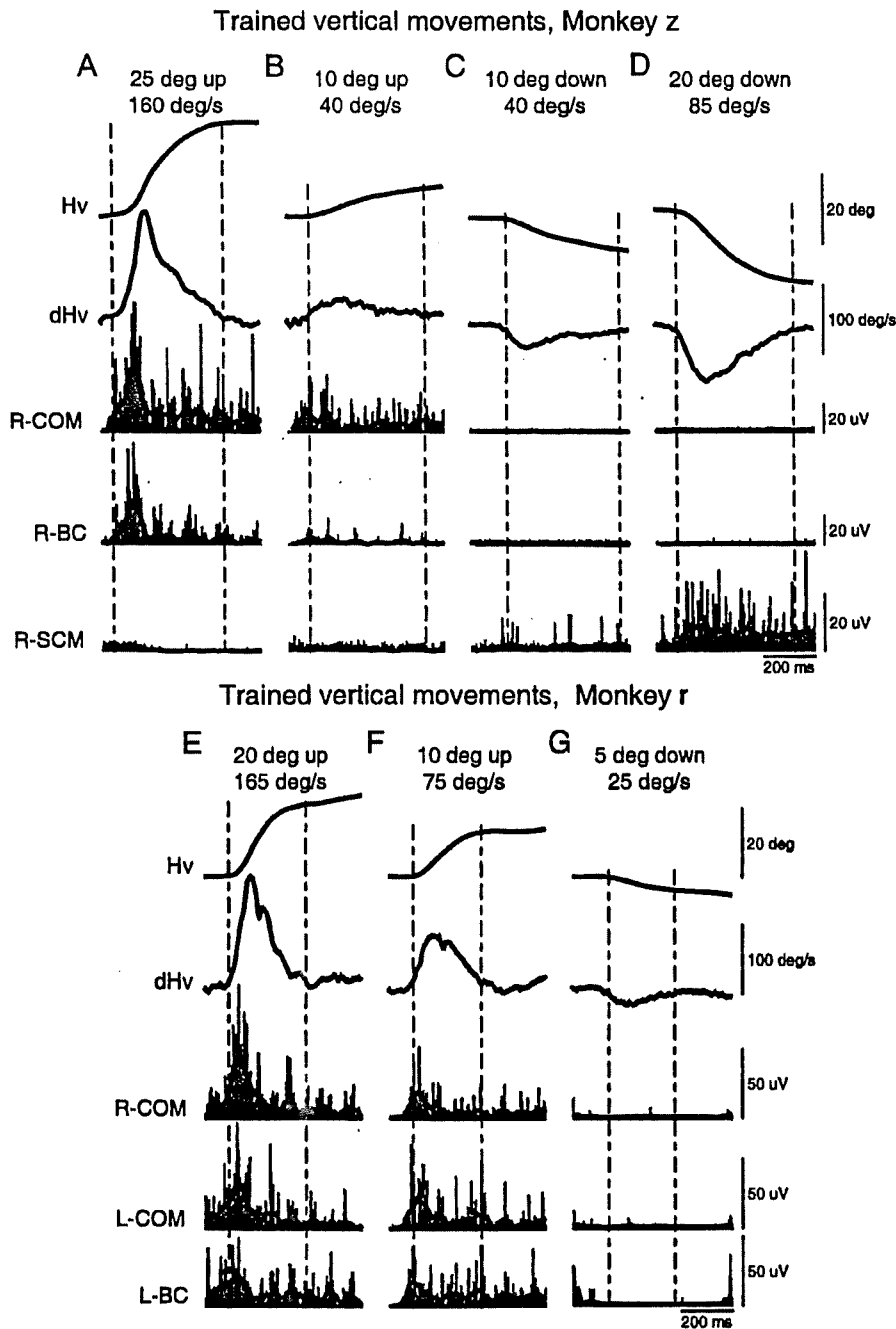


FIG. 11. Vertical head position (Hv) and velocity (dHv) traces, and EMG patterns from *monkey z* (A–D) and *monkey r* (E–G) during movements of various amplitudes and velocities in the vertical plane. All data are from trained sessions. Same format as Fig. 3.

girdle to the spinal column (AS ant, AS post). Figure 17A shows a typical example consisting of seven oscillations over a period of 1 s. All muscles displayed discrete bursting profiles, and had activity levels >60 – $100 \mu\text{V}/\text{bin}$. A closer examination of the temporal aspects of the EMG activity revealed that some muscles burst twice per cycle, whereas other muscles burst only once per cycle (Fig. 17, B and C). In those muscles bursting twice per cycle, the magnitude of the two bursts differed. The synergies identified for rapid turns could be discerned during head shakes, but coactivation was stronger during shakes than turns (e.g., note the bilateral activation in the OCI muscles in Fig. 17B). Strong activation in many muscles often occurred 20 ms prior to the start of the turn toward the preferred direction (i.e., R-OCI and R-SP

burst before right turns; L-OCI, L-RCP maj burst before left turns; Fig. 17C), while these muscles lengthened.

DISCUSSION

This report is the first detailed examination of EMG activation in multiple monkey neck muscles during a large range of head postures and movements. Similar studies in cats revealed that individual neck muscles, and even individual compartments within a given neck muscle, are controlled by the CNS in specific and reproducible ways (Keshner 1994; Keshner et al. 1992; Richmond et al. 1992; Thomson et al. 1994, 1996; Wilson et al. 1983) but revealed complex and somewhat counter-intuitive patterns, as dis-

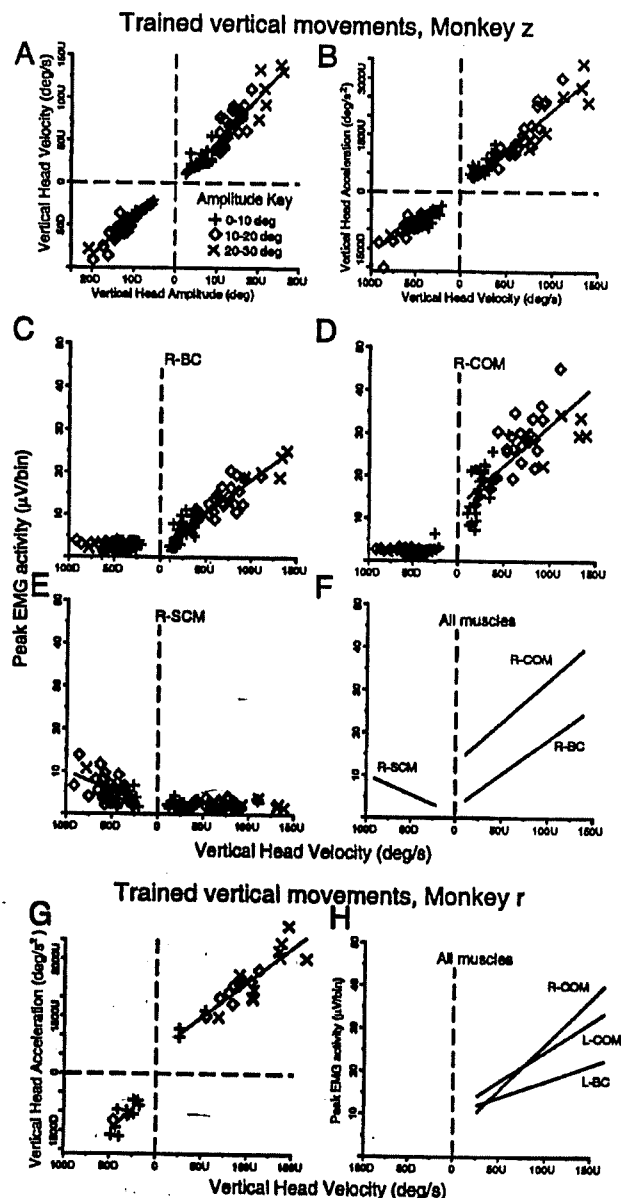


FIG. 12. Relationship of the kinematics and EMG activity during trained movements in the vertical plane from monkeys *z* (A–F) and *r* (G, H). A correlates peak velocity to movement amplitude for monkey *z*; B and G correlate peak acceleration to peak velocity for monkeys *z* and *r*, respectively; C–E correlate smoothed peak EMG activity to peak head velocity for different muscles in monkey *z*; F and H summarize the statistically significant ($P < 0.05$) regression lines for the relationships between various muscles and peak head velocity for monkeys *z* and *r*, respectively. Same format as Figs. 4 and 5. Only trials in which the initial head position was within 10° of center and in which the movement deviated $<20^\circ$ from vertical contributed data to this figure.

cussed in the following text. The activity from analogous muscles in monkeys is similarly specific and reproducible but somewhat simpler to relate to kinematics. This discussion focuses on the similarities and differences between cats and monkeys in terms of the likely kinetics of the various postures and movements and the comparative architecture of the muscles as revealed in the companion paper (Richmond et al. 2001). This approach must eventually be combined with quantitative kinetic and biomechanical analyses of normal and perturbed head movements, as well as single-

unit recording studies in the brain stem, to understand fully the underlying neuromuscular control.

Methodological considerations

To study head movements systematically, we examined head movements generated during trained gaze shifts since these are measured easily and reproduced consistently. However, had we only studied trained head movements, we would not have observed the wealth of variation in EMG activation that accompanied spontaneous head movements. For example, craning movements were associated with coactivation of the two SCM muscles (Fig. 16), which are antagonists during head turns. Head shakes were associated with very high levels of activity in all muscles, apparently phased to contribute to the high accelerations observed during such rapid movements (Fig. 17). General features of these movements were observed by comparing repeated sequences generated over the course of weeks. If future studies are concerned with the neuromuscular strategies underlying such movements, clever ways will have to be devised to elicit many such movements reproducibly.

In this study, we recorded only horizontal and vertical head rotations and not the remaining 4 degrees of freedom (df; torsional rotation and 3 directions of translation). Qualitatively, we observed motion in all 6 df during the natural repertoire of head movements. Translating movements were frequently generated when the monkeys craned for food or tried to visualize objects partially obstructed by barriers. Torsional rotations of varying magnitudes were generated during orienting movements and feeding behaviors but were generally excluded from analysis. Other methodologies, such as three-dimensional coil systems and analysis of reflective and fluoroscopic markers, would be better suited to quantifying such motion and estimating the kinetic implications to better understand the specialization of neck muscle control for these tasks.

Postures and synergies

To hold its head in the central position, the chair-restrained monkey requires little or no muscle activity (Fig. 10), probably because the head is aligned vertically on top of the cervical and thoracic vertebrae so that the weight of the head is borne by compression of underlying vertebrae. Deviations from this "metastable" position required increased levels of muscle activity to balance the head. Interestingly, both statically inclined and declined postures were associated with flexor and extensor muscle activity that was variable but sometimes included some co-contraction of antagonist muscles (Fig. 10).

To hold its head in progressively more turned postures, the monkey was observed to recruit progressively all of the muscles that tended to pull the head into such turned postures. Suboccipital muscles such as OCI and RCP maj were active for even the smallest deviations from center to which activity in multiarticular head turners such as SP cap and SCM was added for more turned postures. Similar trends have been reported previously (Bizzi et al. 1971; Lestienne et al. 1995, 2000) and have been suggested to reflect underlying kinematics: small turns are thought to be executed by rotations at suboccipital joints whereas larger turns require additional rotations about lower cervical vertebrae (Kapandji 1974). Furthermore, some muscles (e.g., RCP maj, SP cap, and SCM) are also involved in

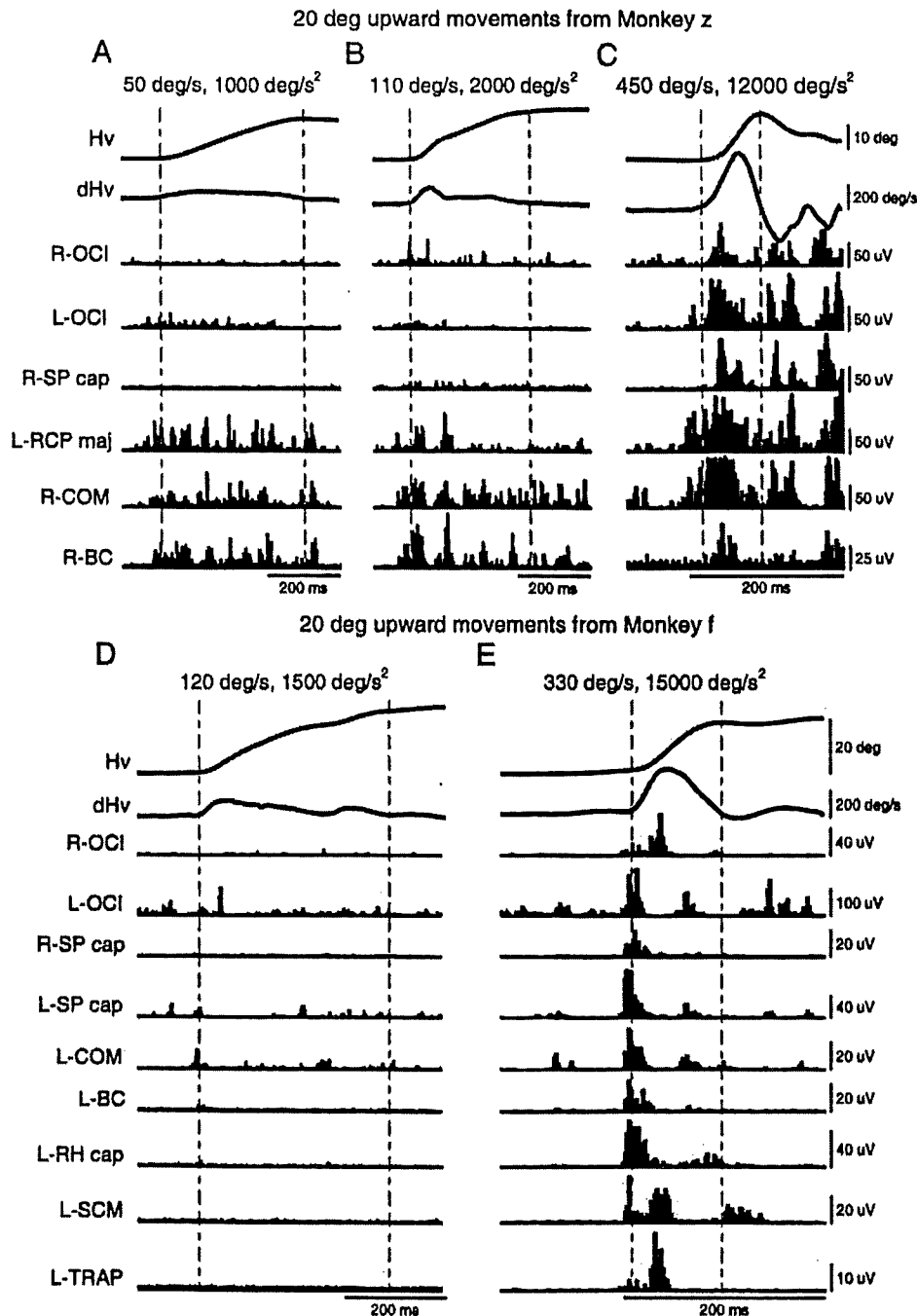


FIG. 13. EMG patterns from *monkeys z* (A–C) and *f* (D and E) during inclining movements of 20° with different dynamics. All data are from spontaneous sessions, and all began near the center vertical position. Note the time scale differs for different movements.

postures and pure movements in the vertical axes. This observation is interesting considering that horizontal and vertical components of head movements appear to be controlled by separate brain stem structures downstream of the superior colliculus (owls: Masino and Knudsen 1990; cats: Grantyn and Berthoz 1987; Isa and Naito 1994, 1995; Sasaki et al. 1999; monkeys: Cowie and Robinson 1994).

The postural activity of some monkey neck muscles was different from that reported for homologous cat muscles (Akaike et al. 1989; Guitton and Mandl 1978; Keshner et al. 1992; Richmond et al. 1992; Roucoux et al. 1980, 1989; Thomson et al. 1994, 1996). The differences may be related to the posture of the cervicothoracic joints, which some of

these muscles cross. Studies in cats are usually conducted with the trunk oriented horizontally and the cervicothoracic column in an S-shaped configuration, whereas studies in chaired monkeys are conducted with the trunk and cervical column oriented more vertically. In cats, BC is active tonically over most of the range of inclined and declined midline head positions, including the central position; in monkeys BC had little activity during tonic postures (Fig. 10). However, BC has been found to become active when monkeys hold their heads in neutral postures during quadrupedal stance when the cervicothoracic region is held in a more S-shaped posture like that in which cats were studied (E. Keshner and B. Peterson, unpublished observations).

Abrupt downward accelerations from Monkey f

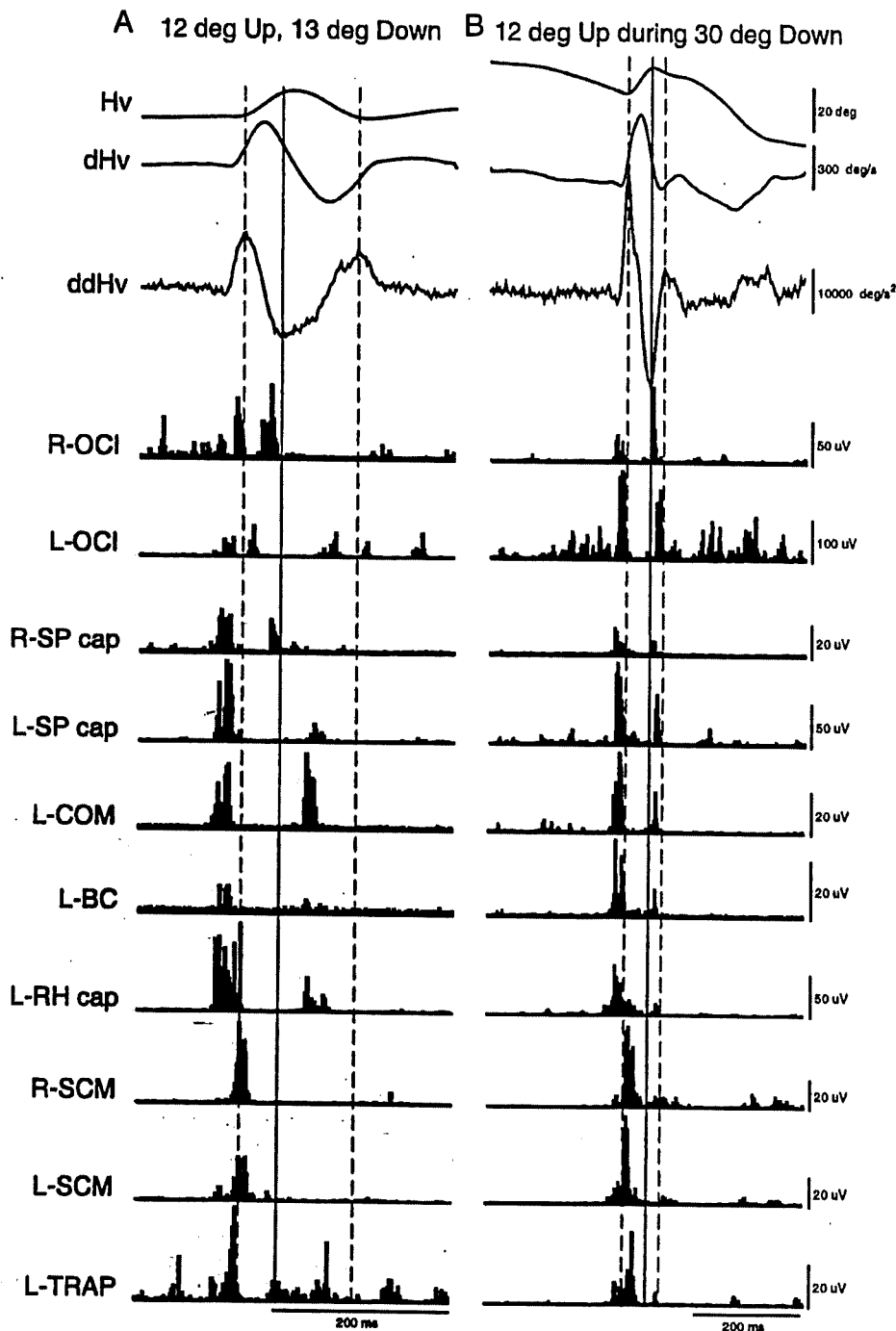


FIG. 14. EMG patterns from *monkey f* during 2 sequences of head movements in the vertical plane, composed of both inclining and declining movements. *A* shows a sequence in which a rapid 12° inclining movement was followed immediately by a 13° declining movement. *B* shows a sequence in which a quick 12° inclining movement was generated in the middle of a 30° declining movement. Hv, dHv, and ddHv label traces of vertical head position, velocity and acceleration respectively. The vertical short-dashed lines are aligned on peak inclining accelerations of the head, and the vertical solid lines are aligned on peak declining accelerations of the head. Note that the time scale differs in *A* and *B*.

Further, large horizontal turns in cats are associated with paradoxical activity in the contralateral COM muscle; in chaired monkeys, COM was active only when it could contribute positive work in inclination or during oblique turns. In the monkey, the long cervical muscles that contribute to large horizontal turns may impose mostly compression forces in addition to the axial rotation of the vertical cervical column; in the cat these muscles presumably produce complex torsional forces along the S-shaped cervical column that may require some degree of cocontrac-

tion for stabilization. The preferential recruitment of extensors contralateral to oblique turns may serve to counteract small torsional rotations (Fig. 15).

When rhesus monkeys move in their natural environment, they do so with weight borne on all four limbs. They have been classified as terrestrial quadrupeds, although they can resort to facultative bipedalism when it is useful (e.g., carrying food) (Napier and Napier 1967, 1985). At rest, they typically adopt a squatting body posture that frees their hands for tasks such as feeding and grooming. The presence of the squatting posture

Oblique movements for Monkey z

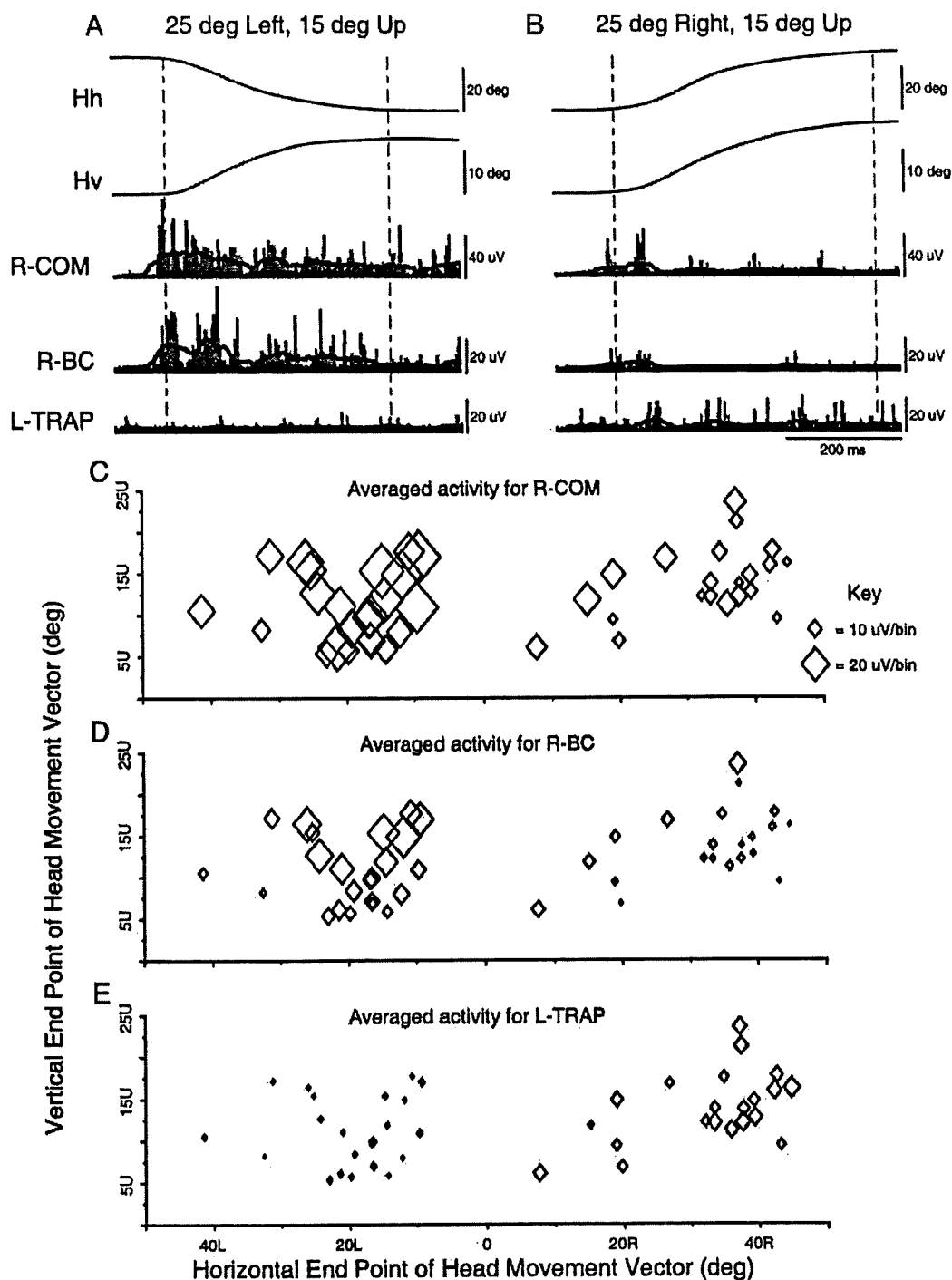


FIG. 15. A and B: horizontal (Hh) and vertical (Hv) position traces and EMG patterns from *monkey z* during either an oblique 25° left 15° up head movement (A) or an oblique 25° right 15° up movement (B). These examples were selected for comparison since they both had inclining components of 15° and approximately equal peak velocities (135–145°/s) but oppositely directed turning components. Note that R-COM and R-BC were more active during the left-up movement than the right-up movement, while the opposite pattern was seen in L-trapezius (TRAP). C–E: relationship between the peak smoothed EMG activity during 45 oblique upward head movements for R-COM (C), R-BC (D), and L-TRAP (E) plotted as a function of the vector of the oblique head movement. The location of each diamond in C–E denotes the endpoint of the oblique upward head movement relative to 0, and the size of each diamond denotes the magnitude of the smoothed peak EMG activity. All data are taken from trained sessions.

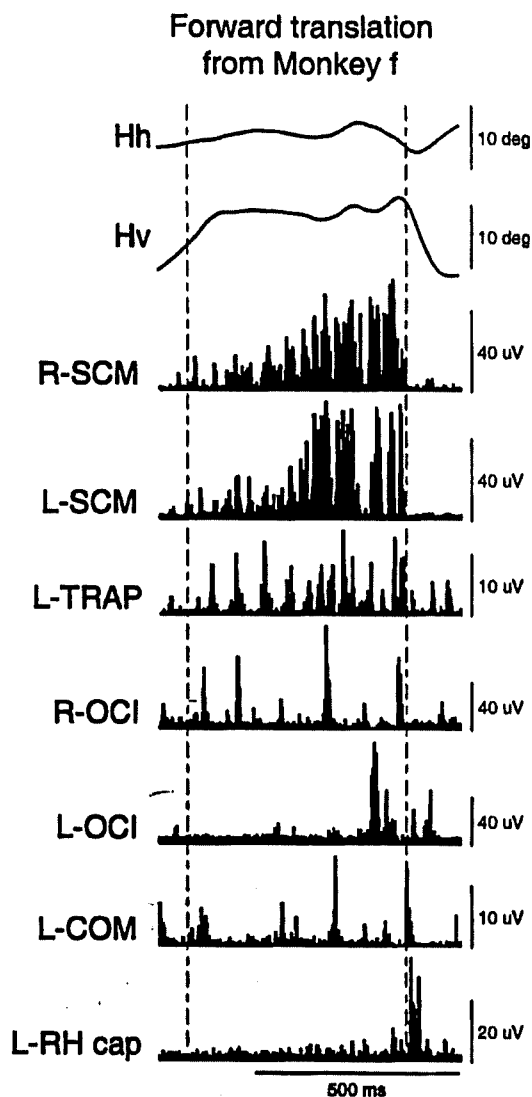


FIG. 16. EMG activity during a head movement made by *monkey f* in which the head translates forward for food during a spontaneous session. The position signals were derived from coil signals and hence do not measure head translation.

and facultative bipedalism has led some to regard monkeys as bipeds to differentiate monkeys from obligatory quadrupeds like rodents and cats (Graf et al. 1995; Vidal et al. 1986). Both the use and anatomy of the monkey head-neck-scapular system are distinct from cats and humans. Compared to cats, monkeys do not use the head as the primary prehensile organ, they have a more modest dorsal neck muscle mass, and they have a scapula attached mechanically to the trunk via the clavicle. Compared to humans, the orientation of the primate scapula is more parasagittal than frontal, and monkeys retain musculature apparently unique to quadrupeds (e.g., RH cap and somewhat separate BC and COM) (Richmond et al. 1999a). These observations do not preclude monkeys as animal models for human head movements, but caution extrapolating results across species.

Because rhesus monkeys are neither obligatory quadrupeds nor bipeds, legitimate concerns may be raised regarding the squatting posture imposed by our primate chairs. Although we

could not measure the orientation of the cervical column directly, a previous study using X-ray photography confirmed that similar craniocervical postures were obtained during squatting in chair-restrained and unrestrained monkeys (Vidal et al. 1986). We reiterate that the activation patterns observed in chair-restrained, squatting monkeys will likely change when monkeys adopt a quadrupedal posture; biomechanical differences between the two postures are likely reflected in distinct uses of at least some of the muscles of the head-neck-scapular complex, particularly those spanning the cervicothoracic junction.

Movements and kinetics

The head movements generated during trained gaze shifts followed simple scaling rules for amplitude, velocity, and acceleration in both the horizontal and vertical axes. Muscle recruitment during these movements appeared to be associated both qualitatively and quantitatively with the presumed kinetic requirements of the movements. The kinetics reflect a mixture of elastic, viscous and inertial force requirements related to position, velocity, and acceleration, respectively, but the covariance of these variables during trained movements makes it difficult to use such data to test hypotheses about neuromuscular strategies. Spontaneous movements exhibited a wider range of kinematic patterns that make it possible to consider the kinetic strategies. This reinforced the notion that neck muscle activation in chaired monkeys is relatively simple to relate to the mechanics and kinetics of head movement.

VARIATIONS IN MOVEMENT DYNAMICS. Head movements during trained gaze shifts were associated with phasic and tonic patterns of recruitment in agonist muscles consistent with overcoming elastic and viscous forces (Figs. 3 and 11). Very rapid movements of the same amplitude were associated with large reciprocal phasic bursts in agonist and antagonist muscles consistent with the requirements of accelerating and decelerating an inertial mass (Figs. 6, 7, 13, and 14). Triphasic patterns of recruitment have been described for rapid arm movements (Hallett et al. 1975; Lestienne 1979; Marsden et al. 1983), and for SCM and SP cap during head movements in humans (Zangemeister et al. 1982). The activation of antagonistic muscles in humans may be a consequence of instructing fast movements. Our results suggest that antagonist muscle activation may be more the exception than the rule, particularly in trained tasks with no premium on either speed or accuracy.

During the fastest movements, the activity of many muscles was not simply triphasic but instead could involve multiple sequences of interleaved bursts in agonist and antagonist muscles during the latter portions of the movement (Figs. 6, 13, and 14). We speculate that the primary agonist and antagonist bursts were part of a preprogrammed, open-loop neural command related to the kinetic requirements of the movement (Fig. 7), whereas the more variable subsequent bursts in the latter part of the movement may reflect the operation of corrective reflexes generated by reciprocally organized neural circuitry and perhaps reflecting vertebral as well as head motion. Such complexity within EMG envelopes cautions against the use of methods that determine the mean of EMG waveforms across similar trials, particularly for the latter portions of the movements. Had we simply averaged our data across multiple trials,

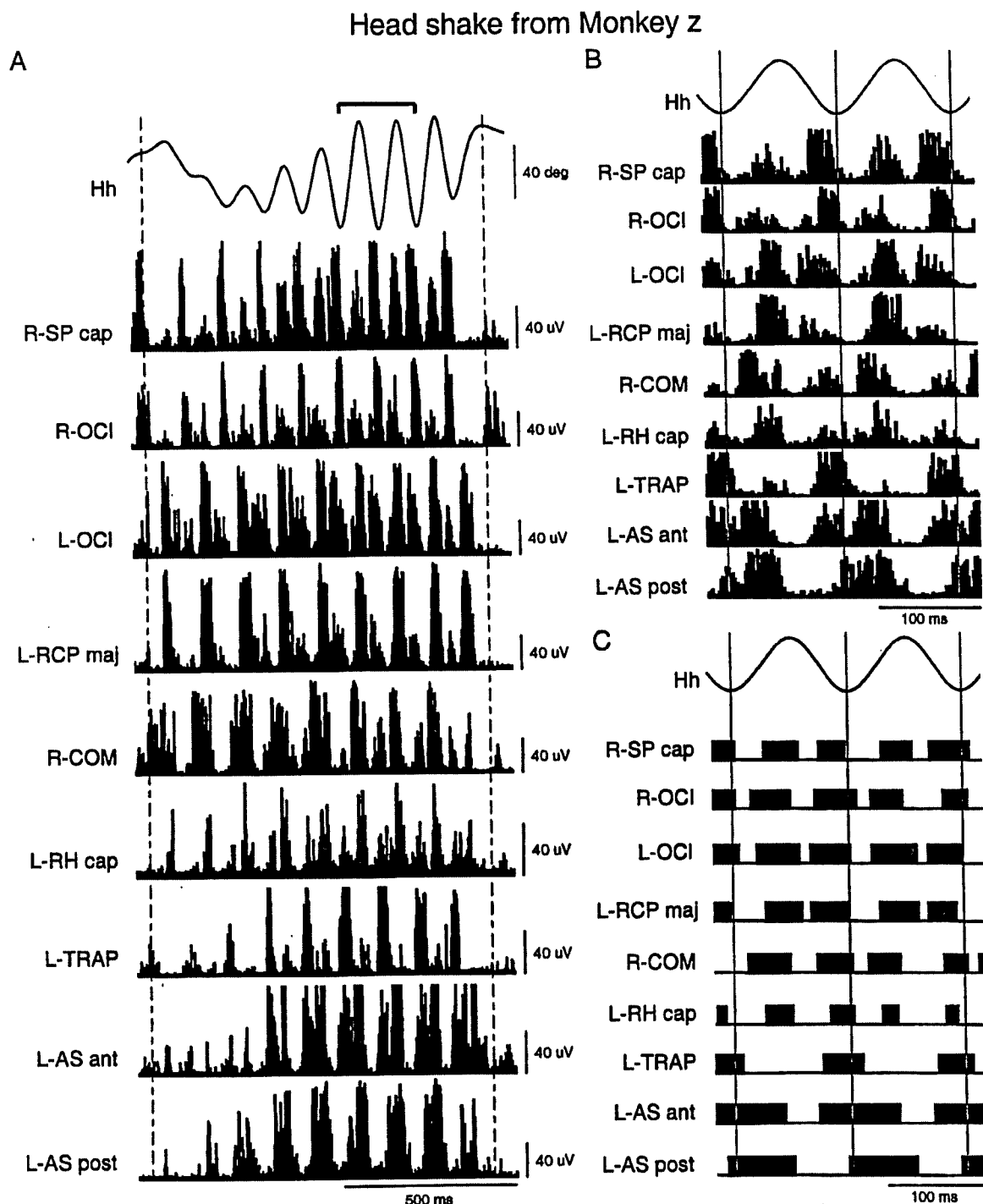


FIG. 17. A: EMG activity and horizontal head position (Hh) traces during a vigorous head shake generated by *monkey z* in a spontaneous session. The vertical dashed lines denote the approximate onset and offset of the sequence. The solid bracket denotes the 2 cycles magnified in *B* and *C*. The vertical solid lines in *B* and *C* demarcate individual cycles of the head shake. *C*: stylized representation of the spatial and temporal EMG activation patterns for the magnified sequence in *B*. The boxes denote the timing of the EMG activity with dark and light boxes signifying relatively higher or lower levels of EMG activity, respectively.

these discrete multiphasic reciprocal bursts would have averaged into a generalized pattern of amorphous cocontraction. Although the observations reported here rely partly on the evaluation of individual examples, an alternative technique would be to deconstruct EMG patterns from multiple trials into the least common waveforms to distinguish aspects of the

signal that are common to multiple movements from those appearing in an idiosyncratic fashion.

CENTRIFUGAL VERSUS CENTRIPETAL MOVEMENTS. Comparisons of centrifugal and centripetal turning movements matched for size and speed revealed that the initial position of the head affected muscle recruitment. The first event preceding centripetal turns

was the silencing of previously active contralateral muscles (Figs. 8 and 9). In addition to releasing stored elastic energy to assist in initiating the turn, the silencing of contralateral muscles may also avoid the high forces that would be required to stretch active muscles: had the silencing of contralateral muscles coincided with the activation of ipsilateral muscles, remnant forces produced by lengthening the contralateral musculature would have resisted the developing turning forces.

The synergy for centripetal but not centrifugal turns was found to include AS ant, which spans from the lateral half of the scapula to the transverse process of C₁. The biomechanical implications of this activity are not clear, but the temporal ordering of recruitment suggests that forces developed by AS ant play a role in the early acceleration of centripetal turns. The involvement of AS ant in centripetal turns is surprising considering this muscle, at least in humans, is viewed commonly as being involved in scapular elevation rather than head turns (Bull et al. 1984; Mayoux-Benhamou et al. 1997). Experimental protocols are often confined to centrifugal movements and would miss such activity.

The temporal activation of agonist muscles also differed between the synchronous activation during centrifugal turns and the staggered recruitment during centripetal turns. Although this report is the first to study temporal relationships in detail, previous studies in monkeys have reported some variability in either the magnitude (Bizzi et al. 1971) or timing (Lestienne and Liverneaux 1988; Lestienne et al. 1995, 2000) of muscle recruitment that appeared related to initial head position. A more complete kinetic analysis will be required to understand such details, which may relate to stability in other axes such as torsion or translation. The later recruitment in ipsilateral OCI and SP cap may also serve to delay their activation until they reach a more advantageous position in the force-length relationship. It is obvious from our results that the central command to individual neck muscles is highly specialized and depends systematically on initial position. Thus it seems inappropriate to produce ensemble EMG activity profiles by averaging normalized EMG activity across multiple neck muscles (e.g., Lestienne et al. 2000).

Muscle architecture

Some differences in muscle function between cats and monkeys may relate to differences in the architecture of individual muscles in addition to the postural differences noted in the preceding text. For example, RCP maj in the cat is almost a pure head extensor. In monkey, its skull insertion is distributed more laterally (Richmond et al. 2001), contributing a turning moment that is reflected in its recruitment during horizontal postures and turns. The gradual loss of distinctive muscle functions that seems to be associated with the tendency to hold the neck and torso in a vertical orientation may be a driving force for the simplification of the primate neck musculature with evolution. For example, COM and BC in the cat are anatomically and functionally distinct (Richmond et al. 1992). In the monkey, COM functions somewhat similarly to BC and often merges anatomically with the anterolateral edge of BC (Richmond et al. 2001). In humans, both muscles appear to have been subsumed into the single muscle semispinalis capitis (Kamibayashi and Richmond 1998).

Cat neck muscles tend to be much more specialized in their

distributions of muscle fiber types than monkey muscles. In the cat, neck muscles range from 10 to 65% Type 1 (slow-twitch) (Richmond and Vidal 1988; Richmond et al. 1999b; Selbie et al. 1993) while the same muscles in monkeys range from 23 to 45% (Richmond et al. 2001). The recruitment of some cat muscles appears to be specialized for tonic postures versus dynamic movements (Thomson et al. 1994, 1996). In the monkey, the neutral head position requires little tonic muscle activity; recruitment during other postures and movements seems related more closely to simple force requirements inferred from the kinematics of the behavior.

Conclusions

The complementary approaches used in this and the companion paper (Richmond et al. 2001) further the understanding of the morphometric, biochemical and physiological organization of monkey neck muscles. Such understanding is important for the development of realistic biomechanical models of head control in monkeys and for future neurophysiological studies on head movement control. Further, this paper emphasizes that monkey neck EMG, at least in the squatting posture, relates relatively simply to the kinematics and presumed kinetics of the movement. This result is heartening for understanding human head-movement control, where most deep neck muscles are inaccessible. However, the central neuromuscular strategies for human head movement cannot simply be assumed from the musculoskeletal architecture. For example, simple "lines of force" logic would not have predicted the sequential activation of muscles during centripetal turns. Although tempered with the knowledge of the differences between humans and monkeys, the study of neck EMG in a squatting monkey at least enables considerations of neuromuscular strategies and cervical biomechanics in a species inclined to adopt a human-like posture.

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REFERENCES

- AKAIKE N, OHNO T, AND TSUBOKAWA H. EMG activities of neck muscles underlying lateral flexion of the neck during head-turning induced by electrical stimulation of the caudate nucleus in cats. *Neurosci Res* 6: 397-410, 1989.
- BAK MJ AND LOEB GE. A pulsed integrator for EMG analysis. *Electroencephalogr Clin Neurophysiol* 47: 738-741, 1979.
- BIZZI E, KALIL RE, AND TAGLIASCO V. Eye-head coordination in monkeys: evidence for centrally patterned organization. *Science* 173: 452-454, 1971.
- BULL ML, DE FREITAS V, AND VITTI M. Electromyographic study of the trapezius (pars superior) and levator scapulae muscles in the movements of the head. *Electromyogr Clin Neurophysiol* 24: 217-223, 1984.
- CORNEIL BD, LOEB GE, RICHMOND FJR, AND MUNOZ DP. EMG activity in dorsal neck muscles of the rhesus monkey during head movements and in different head positions. *Soc Neurosci Abstr* 22: 801.11, 1996.
- CORNEIL BD, OLIVIER E, RICHMOND FJR, LOEB GE, AND MUNOZ DP. EMG responses from primate neck muscles participating in horizontal head movements following stimulation in the superior colliculus. *IVth International Symposium on the head-neck system* (Abstract), 1999.

- COWIE RJ AND ROBINSON DL. Subcortical contributions to head movements in macaques. I. Contrasting effects of electrical stimulation of a medial pontomedullary region and the superior colliculus. *J Neurophysiol* 72: 2648–2664, 1994.
- CRAWFORD JD, CEYLAN MZ, Klier EM, AND GUITTON D. Three-dimensional eye-head coordination during gaze saccades in the primate. *J Neurophysiol* 81: 1760–1782, 1999.
- DEE J AND ZANGEMEISTER WH. Disturbances of antagonistic neck innervation in patients with cerebellar deficits. *J Neurol Sci* 155: 95–103, 1998.
- FREEDMAN EG AND SPARKS DL. Eye-head coordination during head-unrestrained gaze shifts in rhesus monkeys. *J Neurophysiol* 77: 2328–2348, 1997.
- FUCHS AF AND ROBINSON DA. A method for measuring horizontal and vertical eye movement chronically in the monkey. *J Appl Physiol* 21: 1068–1070, 1966.
- GRAF W, DE WAELE C, VIDAL PP, WANG DH, AND EVINGER C. The orientation of the cervical vertebral column in unrestrained awake animals. II. Movement strategies. *Brain Behav Evol* 45: 209–231, 1995.
- GRANTYN A AND BERTHOZ A. Reticulo-spinal neurons participating in the control of synergic eye and head movements during orienting in the cat. I. Behavioral properties. *Exp Brain Res* 66: 339–354, 1987.
- GUITTON D AND MANDL G. Frontal "oculomotor" area in alert cat. I. Eye movements and neck activity evoked by stimulation. *Brain Res* 149: 295–312, 1978.
- HALLETT M, SHAHANI BT, AND YOUNG RR. EMG analysis of stereotyped voluntary movements in man. *J Neurol Neurosurg Psychiatry* 38: 1154–1162, 1975.
- HANNAFORD B, CHERON G, AND STARK L. Effects of applied vibration on triphasic electromyographic patterns in neurologically ballistic head movements. *Exp Neurol* 88: 447–460, 1985.
- HAYS AV, RICHMOND BJ, AND OPTICAN LM. A UNIX-based multiple process system for real-time data acquisition and control. *WESCON Conf Proc* 2: 1–10, 1982.
- ISA T AND NAITO K. Activity of neurons in Forel's field H during orienting head movements in alert head-free cats. *Exp Brain Res* 100: 187–199, 1994.
- ISA T AND NAITO K. Activity of neurons in the medial pontomedullary reticular formation during orienting movements in alert head-free cats. *J Neurophysiol* 74: 73–95, 1995.
- JUDGE SJ, RICHMOND BJ, AND CHU FC. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res* 20: 535–538, 1980.
- KAMBAYASHI LK AND RICHMOND FJR. Morphometry of human neck muscles. *Spine* 23: 1314–1323, 1998.
- KAPANDJI IA. *The Physiology of the Joints. III. The Trunk and the Vertebral Column*. New York: Churchill Livingstone Press, 1974.
- KESHNER EA. Vertebral orientations and muscle activation patterns during controlled head movements in cats. *Exp Brain Res* 98: 546–550, 1994.
- KESHNER EA, BAKER JF, BANOVETZ J, AND PETERSON BW. Patterns of neck muscle activation in cats during reflex and voluntary head movements. *Exp Brain Res* 88: 361–374, 1992.
- KESHNER EA, CAMPBELL D, KATZ RT, AND PETERSON BW. Neck muscle activation patterns in humans during isometric head stabilization. *Exp Brain Res* 75: 335–344, 1989.
- LE GOFF B, MADIC P, LIVERNEAUX P, AND LESTIENNE F. Kinematic characteristics of head trajectory during horizontal movements in monkeys. In: *The Head-Neck Sensory Motor System*, edited by Berthoz A, Graf W, and Vidal PP. New York: Oxford, 1992, p. 510–515.
- LESTIENNE F. Effects of inertial load and velocity on the braking process of voluntary limb movements. *Exp Brain Res* 35: 407–418, 1979.
- LESTIENNE FG, LE GOFF B, AND LIVERNEAUX PA. Head movement trajectory in three-dimensional space during orienting behavior toward visual targets in rhesus monkeys. *Exp Brain Res* 102: 393–406, 1995.
- LESTIENNE F AND LIVERNEAUX P. Muscular synergies of neck muscles during monkey's head movements (Abstract). *J Physiol (Lond)* 406: 33P, 1988.
- LESTIENNE FG, THULLIER F, ARCHAMBAULT P, LEVIN MF, AND FELDMAN AG. Multi-muscle control of head movements in monkeys: the referent configuration hypothesis. *Neurosci Lett* 283: 65–68, 2000.
- LOEB GE AND GANS C. *Electromyography for Experimentalists*. Chicago, IL: University of Chicago Press, 1986.
- MARSDEN CD, OBESO JA, AND ROTHWELL JC. The function of the antagonist muscle during fast limb movements in man. *J Physiol (Lond)* 335: 1–13, 1983.
- MASINO T AND KNUDSEN EI. Horizontal and vertical components of head movement are controlled by distinct neural circuits in the barn owl. *Nature* 345: 434–437, 1990.
- MAYOUX-BENHAMOU MA AND REVEL M. Influence of head position on dorsal neck muscle efficiency. *Electromyogr Clin Neurophysiol* 33: 161–166, 1993.
- MAYOUX-BENHAMOU MA, REVEL M, AND VALLEE C. Surface electrodes are not appropriate to record selective myoelectric activity of splenius capitis muscle in humans. *Exp Brain Res* 104: 432–438, 1995.
- MAYOUX-BENHAMOU MA, REVEL M, AND VALLEE C. Selective electromyography of dorsal neck muscles in humans. *Exp Brain Res* 113: 353–360, 1997.
- NAPIER JR AND NAPIER PH. *A Handbook of Living Primates*. London: Academic, 1967.
- NAPIER JR AND NAPIER PH. *The Natural History of Primates*. Cambridge, MA: MIT Press, 1985.
- RICHMOND FJR, SINGH K, AND CORNEIL BD. Neck muscles in the rhesus monkey. I. Muscle morphometry and histochemistry. *J Neurophysiol* 86: 1717–1728, 2001.
- RICHMOND FJR, CORNEIL BD, AND SINGH K. Animal models of motor systems: cautionary tales from studies of head movement. *Prog Brain Res* 123: 411–416, 1999a.
- RICHMOND FJR, LIINAMAA TL, AND KEANE J. Morphometry, histochemistry, and innervation of cervical shoulder muscles in the cat. *J Morphol* 239: 255–269, 1999b.
- RICHMOND FJR, THOMSON DB, AND LOEB GE. Electromyographic studies of neck muscles in the intact cat. I. Patterns of recruitment underlying posture and movement during natural behaviors. *Exp Brain Res* 88: 41–58, 1992.
- RICHMOND FJR AND VIDAL PP. The motor system: joints and muscles of the neck. In: *Control of Head Movement*, edited by Peterson BW and Richmond FJR. New York: Oxford, 1988, p. 1–21.
- ROUCOUX A, CROMMELINCK M, AND DEOSTRE MF. Neck muscle activity in eye-head coordinated movements. *Prog Brain Res* 80: 351–362, 1989.
- ROUCOUX A, GUITTON D, AND CROMMELINCK M. Stimulation of the superior colliculus in the alert cat. II. Eye and head movements evoked when the head is unrestrained. *Exp Brain Res* 39: 75–85, 1980.
- SASAKI S, ISA T, AND NAITO K. Effects of lesion of pontomedullary reticular formation on visually triggered vertical and oblique head orienting movements in alert cats. *Neurosci Lett* 265: 13–16, 1999.
- SELBIE WS, THOMSON DB, AND RICHMOND FJR. Suboccipital muscles in the cat neck: morphometry and histochemistry of the rectus capitis muscle complex. *J Morphol* 216: 47–63, 1993.
- THOMSON DB, LOEB GE, AND RICHMOND FJR. Effect of neck posture on the activation of feline neck muscles during voluntary head turns. *J Neurophysiol* 72: 2004–2013, 1994.
- THOMSON DB, LOEB GE, AND RICHMOND FJR. Effects of neck posture on patterns of activation of feline neck muscles during horizontal rotation. *Exp Brain Res* 110: 392–400, 1996.
- VIDAL PP, GRAF W, AND BERTHOZ A. The orientation of the cervical vertebral column in unrestrained awake animals. I. Resting position. *Exp Brain Res* 61: 549–559, 1986.
- WILSON VJ, PRECHT W, AND DIERINGER N. Responses of different compartments of cat's splenius muscle to optokinetic stimulation. *Exp Brain Res* 50: 153–156, 1983.
- WINTERS J. Biomechanical modeling of the human head and neck. In: *Control of Head Movement*, edited by Petersen BW and Richmond FJR. New York: Oxford, 1988, p. 22–36.
- ZAJAC FE AND GORDON ME. Determining muscle's force and action in multi-articular movement. *Exerc Sport Sci Rev* 17: 187–230, 1989.
- ZANGEMEISTER WH, JONES A, AND STARK L. Dynamics of head movement trajectories: main sequence relationships. *Exp Neurol* 81: 76–91, 1981.
- ZANGEMEISTER WH, STARK L, MEIENBERG O, AND WAITE T. Neural control of head rotation: electromyographic evidence. *J Neurol Sci* 55: 1–14, 1982.

